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Anatomy of Prepatterns in Plants: A Survey

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Abstract

Prepatterns were initially described independently by Bunning in 1953 for plants and by Stern in 1954 for *Drosophila* with most of the features essentially the same. The one important difference is that in plants the elements of a prepattern are morphologically recognizable whereas in animals they are detected only indirectly. Two kinds of prepatterns in plants are (a) *replacement* where elements of a prepattern are substituted by more differentiated elements in the pattern and (b) *copy* where a pattern forms near the prepattern and both are adaptive but in different ways. A case of replacement is where meristemoid cells in the prepattern are exchanged for stomata in the pattern and an example of copy is the vein pattern in watermelon mesophyll gives rise to nearby stripes in the epidermis. Both replacement and copy prepattern-pattern dualities occur at different levels of plant organization from cell components (thickened vertices in collenchyma) to individual plants (plantlets along the margin of the *Bryophyllum* leaf). Comparative morphoanatomy of vascular plants finds similar patterns to both lower plants and animals suggesting these features are conserved in the former and had independent origins in the latter.

Keywords: prepattern, pattern, plant development, evo-devo, vascular tissue

1. The Concept of Pattern

Development of plants and animals is an integration of cell differentiation and pattern formation both telescoped out by cell proliferation and growth. As differentiation produces something new, patterning distributes these new entities in space and over time. Although differentiation and patterning are strongly coupled, Bűnning (1953) introduced the concept of meristemoid which is a meristematic cell in plants that differentiates into small specialize structures such as a stomatal apparatus of five to eight cells, a trichome of one to more than three cells or a cotton fiber of two cells. Which fate a meristem assumes depends upon the competency of the background cells The description of this concept of Bűnning's work as translated from German by Foster (1956) is "meristemoids are qualitatively alike and hence they depend upon later factors, which as yet have not been analyzed, whether meristemoids of the epidermis forms a hair or a stoma, or whether meristemoids in the inner tissue gives rise to a raphide, an oil cell or a sclerenchymatous idioblast." While a meristemoid gives rise to a specialized structure, its deployment remains the same.

Later Stern (1954) observed that the type of units in an adult pattern is independent of the pattern itself. He found through studies of genetic mosaics in *Drosophila* that fields of cells having different alleles respond differently to the same prepattern suggesting there are two steps in pattern formation (1) a prepattern forms which is composed of prepattern elements and (2) these elements then specialize further according to the type of background tissue present while their deployment remains unchanged. This scheme in animals is identical to that of Bűnning for plants with the difference between prepatterns of plants and animals is that in the former the prepattern elements are visible such as meristemoids and that in the latter specialized cells are invisible and therefore more speculative. Also, Stern used the term prepattern whereas Bűnning didn't although the special aspect of a meristemoid is implied.

Before developing the concept of prepattern the idea of a pattern needs to be discussed. From the old French for father (patron) and then into Middle English the term pattern took on several different meanings of imitation including the recursive idea of repetition including its mathematical meaning in geometry. In developmetnal biology a pattern is commonly considered as anything repeated in a predictable fashion through space and/or time but can be stretched to include gradients. A simple type of pattern is a repetitive occurrence of an element in

two dimensions in a common field as polka dots (Figure 1A) and this arrangement is also seen in two dimensions in the deployment of stomata on a leaf (Figure 1B). Here the elements, cells as meristemoids, give rise to stomatal apparatuses and this case is an example of what is called here a *replacement* pattern where the original prepattern elements, the meristemoids, no longer exist but are replaced by other type(s) of element(s) such as stomata. A replacement pattern in three dimensions would be a sponge (Figure 1C) with spaces somewhat uniformly arranged. Botanically a 3D plant pattern is the arrangement of phenolic cells in the root of *Brosinum* (Jacomassi, Moscheta and Machado, 2007; here Figure 1D). A second type of pattern can be called a *copy* in which the prepattern elements dictate where the pattern elements form; the prepattern elements remain as they have their own adult function. An example of a copy prepattern is the front-back bilateral, or dorsal-ventral, asymmetry of a man on which another asymmetry is added, that of the two street signs he wears (Figure 1E). Botanically a case of a copy prepattern is that for leaf veins which are for moving fluids and serve as a prepattern for formation of trichomes in the epidermis only directly above veins and functionally for protection early in development (Volkama et. al., 2003; here Figure 1F).

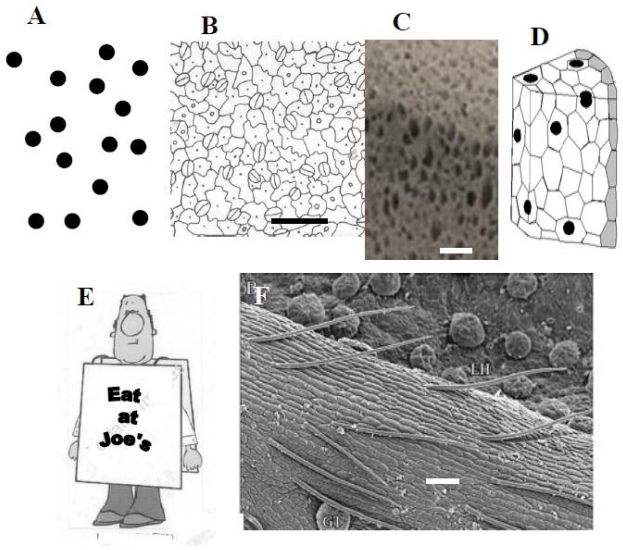

Figure 1. Types of prepatterns. A: A 2D replacement type of prepattern of polka dots. B: Replacementpattern of stomatal arrangement. Bar is 400 μm. C: 3D replacement pattern of a sponge. Bar is 7 mm. D: 3D plant replacement pattern of root cortex of *Brosimum* with dark phenolic cells. After Jacomassi, Moscheta and Moschado (2007). E: A copy prepattern of man and signs. F:A plant copy prepattern of veins bearing long trichomes in *Betula punescens* var. *pubescens* (Valkama et. al., 2003). Bar is 120 μm.

An interesting case of patterning is that of collenchyma where vertices are thickened with cellulose (Figure 4a). Here the pattern is cellulose thickening and the prepattern is the vertex which is the intersection of two anticlinal walls. This would be a case of copy where both arrangements persists.

2. Recognition of Prepattern

Prepatterns can be recognized by several means, (a) mutation, (b) coexistence of prepattern and pattern and (c) one prepattern for several different patterns that develop in sequence. Mutation is most effective but difficult to obtain. Stomates in *Arabidopsis* seem to have a typical means of arrangement (Geisler et. al., 2000). A meristemoid mother cell (MMC) divides unequally to form a small meristem daughter cell that forms a stoma and a large daughter cell that may or may not behave as a MMC. This process of MMC continues for two more cell divisions. The patternization process leads to each stoma separated from other stomata by at least one cell. By the criteria established in this study the MMC of the literature is actually a meristemoid of the prepattern and the meristemoid of the literature is an initial cell because a meristemoid is what creates the spacing feature. Patterning of elements can be separated from features of these elements by mutation (Wang et al., 2007). Mutant MKK5RNAi protein has all epidermal cells converted into stomata and mutant GVG-Nt-MEK2^{DD} has only pavement cells, both are alterations of pattern while mutant MKKARNAi has separated clusters of two or three stomata so is a change in element structures of another kind while retaining the original pattern of deployment. Similarly and also in *Arabidopsis* Larkin et al. (1994) recognized two kinds of mutations of trichomes, those altering pattern and those altering development of individual trichomes. In the case of the former mutations lead to fewer and more widely spaced trichomes. Also in *Arabidopsis* Schnittger et al. (1999) found the mutant *try*

gene leads to clusters of about four trichomes instead of the wild type solitary trichomes (Figures. 2A and B). This too is a case of deviation of elemental development rather than a change in prepattern.

As shown above mutants commonly leading to a cluster of elements from one meristemoid are found for stomata such as *too many mouths* mutation (Geisler et al, 2000), trichomes (Pesch & Hülskamp, 2011) and stomata in many wild type taxa of begonia (Lau and Korn, 2007).

A second means of identifying a prepattern is that its elements are morphological and in a copy configuration. For example, some varieties of the orchid *Paphiopedilum* have tessellated leaves, dark green quadrilateral areas lying over cross-veins (Figures 3A and B). Here the prepattern arrangement is that of cross-veins, structures that are patterns in themselves as functional in efficient transport and support, and the secondary pattern is tessellation in providing camouflage. Another example is major veins in watermelon lying beneath stripes indicating the arrangement of veins, again, is a prepattern and that for stripes is the pattern (Korn, 2007; here Figures 3C and D). Most likely some specialized or meristematic cells of these vascular bundles are specifically the prepattern elements. Here in both cases prepattern and pattern remain into the adult organ as different and spatially separate structures unlike the replacement case where prepattern units are replaced by pattern units. The spatially separate occurrence of prepattern and pattern is the motive for proposing a new kind of prepattern, the copy prepattern as described above.

A third method for identifying a prepattern apart from the pattern is when the same prepattern generates several different patterns. An example is the pattern of files of root hairs in the epidermis of the maturation region of the root and a similar arrangement of stomata in the epidermis of the hypocotyl in *Arabidopsis* (Webb, 2002; here Figures 3E -H; Korno et. al., 2007; here Figure 3I) . In both cases the specialized structures appear in larger epidermal cells overlying two even larger cortical cells. It has been found that cortical cells inhibit specialization (Takahashi et. al., 2003). Here the copy prepattern is the arrangement of hypodermal cortical cells which is coupled to different kinds of cell differentiations, a hair in the root which is a part of a cell and the stomatal apparatus in the hypocotyl, which is a multicellular structure. This common prepattern to several patterns is altered in the mutant *ttgi* plant which has both modified rows of hairs in the root and stomata in the hypocotyl (Hung et al, 1998) (Figures 3E-H), a multiple deviation fulfilling both the first and third criteria of genetic modification of prepattern and multiple associations of the prepattern with other patterns. Bean et al. (2002) found the arrangements of trichomes and stomata in the mature cotyledons of *Arabidopsi*s appear to be the same and both are altered similarly in *gl1* and *try* mutant plants. Here the same replacement prepattern preceding two different patterns can be altered in the same way by a common mutation.

Another example of multiple patterns from the same prepattern but sequentially occurring in the same tissue is that for trichomes and stomata in the tobacco leaf (Figure 3j). The degree of order is the R value that can be measured by the method of Clarke and Evans (1954). Their equation is $R = 2NN \cdot D^d$ where D is density, or elements per unit area, and d is the number of dimensions. An R value of 2.15 is perfectly ordered (space filling hexagons), that of 1.00 is random (raindrops on a sidewalk square) and one near zero is clustering (dancing partners). R values of 1.265 for trichomes and 1.261 for small glands from sample sizes of 25 from Kunkel indicate decided ordering. Trichomes are separated by an average of 61.3 μm, and for stomata the average is 35.3 μm. These values give the number of cell generations separating elements in these two pattern formations of 2.0 x log (61.3)/log (35.3), or 2.0 x 1.15 generations, 2.3 cell generations of cell proliferation separate the time when these pattern elements formed. The value 2.0 is used because it takes two divisions for nearest neighbor cells to be separated by one cell in both X and Y directions. In the case for *Haplopappus* (Mauseth, Fig. 10.2, 1988) trichomes, glands and stomata appear sequentially during leaf development. Data collected from this photograph give glands and stomata average nearest neighbor distances of 88 μm and 31 μm, or are separated by 2.0 x log(88)/log(31) or 2.6 cell generations. Likewise, the nearest neighbor distance of trichomes is 152 um and for glands is 88 um or they are separated by 2.2 divisions. The R value for trichome arrangement is 1.41, for glands it is 1.44 and that for stomata it is 1.44. Since all three patterns are approximately the same it seems they come from the same prepattern mechanism, namely heterotypic induction, that is, a differentiated cell inhibits contiguous cells from becoming differentiated. Trichomes often have many contiguous cells arranged in radial fashion indicating they form early in leaf development before epidermal cell division ceases (Figure 2C).

An important question is what patterns do not come from prepatterns? A likely case of altered pattern is that of heterocyst formation in the blue-green alga *Anabaena*. Wild type filaments have few, solitary heterocysts separated by about ten vegetative cells. The multicopy *hetR* strain forms heterocysts in clusters (Builema and Haselkorn, 1991; here Figures 2D and E) and since clusters are spaced like the wildtype heterocysts pattern this mutation is not a change of prepattern but a change in fate of individual elements. If a special precursor cell to heterocyst formation exists then it would serve as an element of a prepattern.

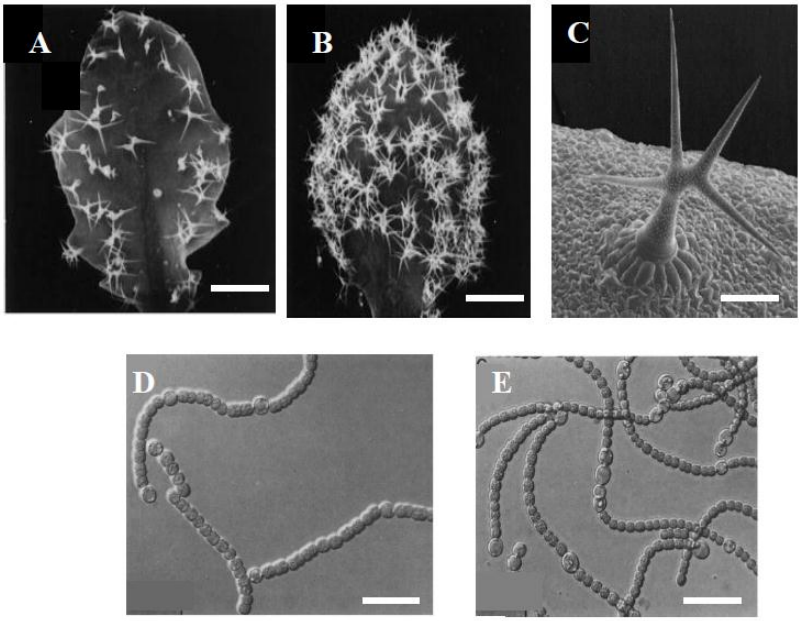

Figure 2 A: Trichomes of wild type leaf of *Arabidopsis*. Bar if 0.5 mm. B: Clustered trichomes on mutant *try* leaf. Bar is 0.5 mm. C: Wild type trichome surrounded by many radial epidermal cells. Bar is 100 µm. Figures (a) – (c) from Schnittger et al. (1999) courtesy of American Society of Plant Biologists. D: Wild type filaments of *Anabaena*. Bar is 10 µm E: Filaments of multicopy *hetR Anabaena* with heterocysts more clustered than in wild type filaments. Bar is 10 µm. Figures D and E from Buikema and Haselkorn (1991).

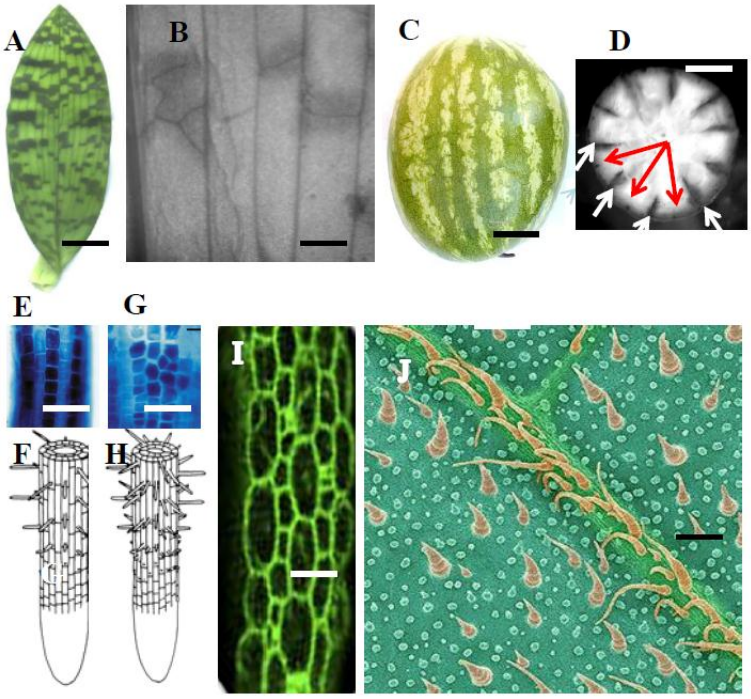

Figure 3. A: Tessellated *Paphiopedium* leaf. Bar is 12 mmB: Cross-veins of *Paphiopedium* beneath quadrilateral pigmented areas. Bar is 2 mm. C: Stripped watermelon. Bar is 5 mm. D: Clustered stomata in *Begonia* X *semperflorens*. Bar is 100 µm. E: GUS staining of trichoblasts of *Arabidopsis* root. Bar is 50 µm. F: Diagram of surface of *Arabidopsis* root with alternating wide files with root hairs and narrow files without root hairs. G: All files of root with atrichoblasts. Bar is 50 µm. H: Diagram of mutant with root hairs in all cells. E and G from Webb et. al., 2002; F and H from Wada et. al., 2002. I: Surface of hypocotyl with wide cell files and narrow cell files. Bar is 50 µm. From Kono et. al., 2007. J: Abaxial surface of *Salvia divinorum* leaf with well-spaced large trichomes (white arrow) and closer spaced small glands (black arrow). Bar is 2 mm. Courtesy of Dennis Kunkel.

Theories also can be analyzed by the three prepattern criteria. Is there a prepattern for vein development? Two major ideas have been developed to explain vein formation in leaves. One is the canalization idea of Sachs (1991a and b) and recently supported by Rolland-Lagan et al.(2004) in which auxin flows intercellularly leading to constant changing of the flux status of each cell wall. The more auxin passes between certain pairs of cells the greater the diffusion coefficient as a positive feedback relation. As Sachs noted, there is no prepattern here because the entire vein forms directly from unspecialized mesophyll tissue elements.

The case of stomatal deviation is also problematical. The *stomatal density and distribution* mutant in *Arabidopsis* has more stomata and are closer (Berger and Altmann, 2000). This could be explained directly as a change in timing. On the other hand, Yang and Sack (1995) found two mutations in *Arabidopsis*, *too many mouths* (*tmm*) and *four lips* (*fl*), which alter the deployment of normal stomata to more clustered patterns. The question then is the prepattern altered or the fate of a single meristemoid changes to form several clustered stomata? It seems the latter is an easier interpretation so these mutants tentatively are not tests of prepattern alteration. Shoot regeneration presents another problem. A destroyed stem apical meristem (SAM) can lead to new shoots arising from lateral buds which, in turn, arise from leaf primordia. The stem is the prepattern for leaf pattern which, in turn, serves as a prepattern for the bud patterning as a second pattern which is also a prepattern for the branching pattern. However, in sunflower an X-ray damaged SAM might also lead to regeneration of a new SAM from nearby cells directly (Lagenauer and Davis, 1973) without any prepattern required. In general, numerous adult patterns are insufficiently understood to know if prepatterns are involved such as cases of location of xylem and phloem in vascular bundles, or perhaps alternating nodes and internodes along stems, placement of ovules in the ovary and formation of laticifer networks in vascular tissue.

The arrangement of barb cells along the margin of the elodea leaf seems to be another case of pattern formation without a prepattern. At first all marginal leaf cells begin to bulge out at the distal end of external facets followed by cell division where proximal cells are normal epidermal cells acting as spacers between distal barb cells (Figures 5C and D). Spacing between barbs is achieved by cell proliferation of cells to seemingly form the pattern without a prepattern. A closer look leads to a different answer. The initial cell bulges out at the distal end due to some cytoplasmic factor (particle?) attached to the distal region of the outer facet which stays put during cell division and this intracellular polarity serves as the prepattern for intercellular polarity.

3. Levels of Patterns Arising from Prepatterns

It is important to see what the levels of pattern are that come from prepatterns as this relationship indicates how significant prepatterns are in the overall development of higher plants. It will be shown that these levels range from those of a cellular component to the whole plant, or individual, indicating they have played a major role in evolution, The series of levels noted here, cell, cell complex, tissue, tissue complex, organ, organ system and individual has been discussed previously (Korn, 2002).

3.1 Cell Component

Collenchyma is a supporting tissue with thickened vertices. As a pattern the distribution of vertex thickenings which has a Clark and Evans R index of 1.15, that is, slightly ordered (Figure 4A). The prepattern is the distribution of cell vertices which in 3D is actually intersections of facet edges. Another example of an intracellular pattern is finger-like outgrowths of epidermal cell facets (Figure 4B, Korn, 1976). The number of ingrowths and outgrowths is 4.01and 3.94, respectively, suggesting four cytoplasmic particles per cell that form outgrowths. The prepattern is then the placement of these hypothetical particles and the pattern is the deployment of localized growths.

3.2 Cell

It would seem that placement of one unique cell during multicellular plant development is almost a contradiction of a pattern but at least one good case can be found. The location of the egg in the female gametophyte, or embryo sac, is critical for successful fertilization. That it is placed at the micropylar end and at the margin allows for male gamete fusion with the egg nucleus directly. Is this a case involving a prepattern or by some other means, such as cell lineage? Willemse (1981) describes a polarity in the embryo sac according to location of cell constituents running along the chlazeral-micropylar axis. Some gradient serving as a prepattern mechanism would best explain this polarity. Wolpert (1969) sees a gradient serving as a prepattern if some singularity was present such as the points of either the highest or lowest concentrations of a morphogen in the gradient. By this reasoning the egg is a case of copy prepattern because the structural source of the gradient is the prepattern and the basal location of the egg is the pattern within the gradient.

The egg cell in the Archegonates (ie., liverworts, mosses, ferns and fern allies) would also qualify as an example of a one-celled pattern with a prepattern. As with the egg in the embryo sac, the cryptogamic pattern is the location of a unique cell in a structure, here an egg cell is located at the base of the neck-venter canal of the archegone. The neck-venter canal is filled with fluid forming a gradient of some attractant solute. Evidence for a prepattern within the archegone, such as a gradient found in the embryo sac, remains wanting.

3.3 Cell Complex

A cell complex is a group of cells with a specific function found within a tissue such as a cotton fiber composed of two cells, a basal cell and a cotton fiber (Figure 4C). A stomatal apparatus is composed of two guard cells and several subsidiary cells. Other epidermal derivatives include the peltate gland which includes a basal cell, a stalk cell and several glandular cells as well as some trichomes, those composed of several cells in tandem. A quantitative trait is the number of stomata in a cluster as in *Begonia X semperflorens* (Figure 4D). The number of stomata in a cluster follows a Poisson distribution, a type of random pattern (Lau and Korn, 2007). This number of stomata per cluster is highly correlated with the size of the cell that gives rise to the cluster by comparing the probability distribution of cell sizes to that of the Poisson of stomata/cluster (Figure 4E). Here the prepattern is cell size of the cluster meristemoid and the pattern is the number of subsequent stomata per cluster.

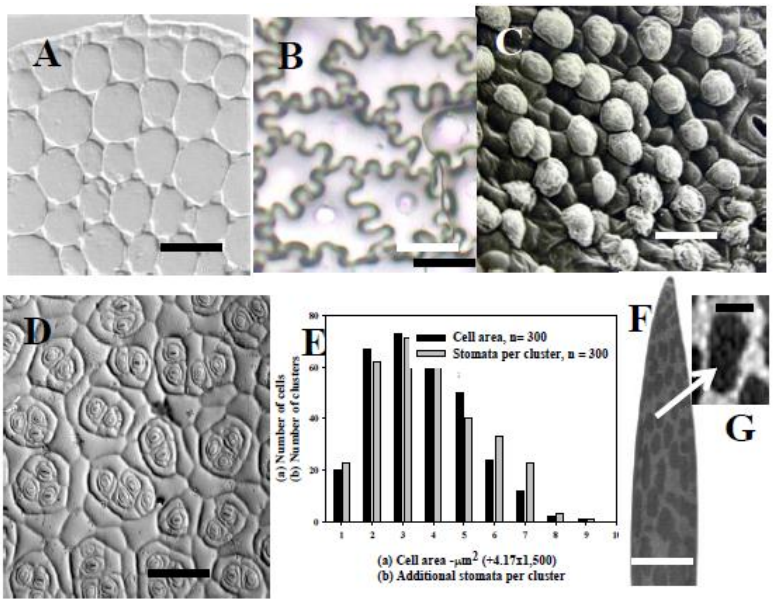

Figure 4 A: Collenchyma tissue with thickened vertices. Bar is 240 μm. B: Finger-like growths on anticlinal facets. Bar is 100 μm. C: Arrangement of young cotton fibers. Bar is 150 μmD: Stomatal clusters of Begonia bracteosa. Bar is 300 μm. E: Graph for correlating cell size and number of stomata per cluster. F: and G: Spots on dorsal surface of a Ledebouria leaf with some overlapping of spots. Bars are 10 mm and 2 mm, respectively.

3.4 Tissue

The mesophyll in monocots is associated with photosynthesis. A rare secondary feature of the mesophyll is the tessellation pattern of light and dark green quadrilaterals noted earlier in the leaf of many varieties of *Paphiopedilum* orchids (Figures 3A and B). Correlated with the dark quadralaterals are cross-veins running laterally between parallel major veins. Since cross-veins form prior to the pigmented quadralaterals the former appears prior to the latter. Cross-veins are a visible copy prepattern to the tessellated tissue pattern.

A stripe in watermelon is a longitudinal array of epidermal pigmented cell clones (Korn, 2007). Each clone is dark green at its margin and light green in the center. Below each longitudinal stripe is a longitudinal vascular bundle in the mesophyll (Figures 3C and D). As in the case of the orchid leaf above, arrangement of vascular bundles in watermelon serves as the copy prepattern for the pattern of a set of stripes.

An instructive case of a prepattern is the somewhat oval green spots on the adaxial leaf surface of *Ledebouria socialis* L. (Figures 4f and g). The nearest neighbor distances between spot centers gives an R value of 1.29 by the method of Clark and Evans (1954), clearly indicating an ordered pattern. Spots can be explained by an initial meristemoid cell either (a) proliferating into a cell lineage of dark green cells, namely, an oval-shaped clone or (b) producing a morphogen that diffuses out to differentiate cells thus forming a dark green spot. It seems

interpretation (b) is correct as spots often overlap, a feature not possible by adjacent cell lineages. To explain the distribution of spots requires a second morphogen which inhibits cells from becoming meristemoids which is the basis for the observed ordering.

3.5 Tissue Complex

A tissue complex is a coordinated set of tissues such as a vascular bundle with tissues of procambium, xylem, phloem, cambium and sometimes laticifers. These tissues arise from procambial strands, hence, the arrangement of xylem, phloem and cambium is the pattern that is derived from some unknown arrangement of procambial strands. Xylem and phloem are sited in stems, leaves and roots with respect to procambium and cambium. In monocot stems prepattern appears to be in bipolar procambial cells (Korn 2016b).

3.6 Organ

Lateral roots form at loci in the pericycle adjacent to xylem arms resulting in files of branch roots equal in number to that of xylem arms. The evidence of the pericycle as the prepattern for root initiation is morphological (Esau, 1940) but which cells of the pericycle are determined to form a root is partly dictated by an oscillating gene (Van Norman et al., 2013).

The pattern of branch stems is from the prepattern of lateral buds which is derived from the prepattern of leaf arrangement. The origin of leaves is problematical as there is evidence it is from concentration of morphogens derived from previous leaves (Mattsson et. al., 2003; Kuhlemeirer, 2007) but also there is evidence for the stem vascular bundle arrangement is the prepattern (Larson, 1975; Korn, 2006a). In either case the arrangement of leaves is the pattern and either auxin concentration or arrangement of vascular bundles is the prepattern.

3.7 Individual

The highest level of development is the individual plant. One type of asexual reproduction is the formation of plantlets along the leaf margin of *Bryophyllum daigremontianum*, Figure 5A). Plantlets form in interseriate regions which then serve collectively as the prepattern for the arrangement of new plants.

3.8 Various Levels

One prepattern serving as the platform for patterns at various levels is the marginal band of all leaves (Korn, 2003). It is the site for association with different mechanisms such as for the marginal growth meristem and pigmentation (tissue), serration and lobes (tissue complexes) and plantlets (individual). This marginal band prepattern can be identified morphologically where it is expected to occur as specialized epidermal cells intercalated between abaxial and adaxial epidermal tissues along the edge of leaves (Figure 5B).

In general, prepatterns give rise to patterns at various levels of organization.

While pattern elements occur at all levels of development, at what levels do prepattern elements occur? This element can be (a) at the cell level in the cases of egg, meristemoid and branch root, (b) at the cell complex level in orchid leaf tessellation, watermelon stripes and root hair locations, (c) tissue complex according to the vein theory of phyllotaxy and (d) at the organ level in seed arrangement and the surface theory of phyllotaxy. As with pattern, prepattern seems to occur at many different levels in plant organization.

4. Origin of Prepatterns

The origin of a pattern is a prepattern but what is the origin of a prepattern? For example, a stoma in a replacement pattern is a meristemoid of a prepattern and the order in a pattern is from the order in a prepattern but where does this prepattern order come from? It is assumed that this order does not come about spontaneously as suggested by some (Sachs, 1969; Feller, 2016) but from transfer of some preexisting order. A meristemoid can be seen as having three kinds of features, cell type, spacing and timing, that are pertinent to explaining prepattern (Table 1). At first a meristemoid comes about spontaneously by cell differentiation (cell type) from an unspecialized epidermal cell and then it divides unequally three times to form three daughter cells isolating the final meristemoid from later meristemoids and cells in a field are induced independently as to where (spacing) and when (timing) to become stomatal initials. Prepattern order then comes from directed unequal cell division as cell spacing mechanism.

Table 1. Types of Prepattern-patterns and Their Features.

Types	Features		
	Example	Spacing	Timing
Replacement			
1. Polka dots (become stomata)	Meristemoids	Intensive	Sequential
Extension			
2. Unbranched (become stomata)	Procambia	Extensive	Sequential
3. Branched (become branches)	Nodes	Extensive	Sequential
4. Copy (becomes watermelon stripe)	Vein		Simultaneous

The introduction of numerous meristemoids creates new relationships that are extensions of those in single meristemoids such as the special relationship between stomata which are never contiguous, meaning that there is order is transferred to how stomata are deployed. This order is seen in the R index of Clark and Evans, $2NN{\cdot}D^{d}$, where NN is the nearest neighbor distance, a features derived from how subsidiary cells are placed between meristemoids. In this example of stomatal patternization the origin of prepattern, and so pattern, is found within singular stomatal apparatuses. Initially a few meristemoids are formed in a field of epidermal cells making NN large and D small or R close to 1.0, or is a random pattern, but as more meristemoids are added between existing ones intensively with R reaching a value around 1.65, notably an ordered pattern much like polka dots (Table 1).

Another spacing mechanism is cell inhibition as found for cotton fibers (Figure 4C), trichomes (Figure 2A) and idioblasts (Figures 1C and D). An initial meristemoid inhibits adjacent cells from becoming meristemoids (heterogenetic induction) thereby separating any meristemoid later formed (Korn, 1994). Here order is transferred from cell-cell inhibition to element separation with an R index of Clark and Evans about 1.65.

A different type of replacement pattern is the parallel arrangement of veins in monocot leaves (Korn, 2016a). They form in two ways, first, as a growing leaf expands adjacent parallel veins separated from each other and when they are a certain distance apart an intercalary vein starts as a new procambial cell (Korn, 2016a). This feature suggests veins produce an inhibitor laterally of any new veins forming implicating mesophyll cells are enlisted through homotypic induction (like induces like). A second process is the addition of procambial cells at the end of a vein. A vein seems to extend step-wise as found by GUS staining trap lies (Holding and Springer, 2002; Kang and Dengler, 2004; Scarpella et al., 2004; Scarpella and Meijer, 2004) where preprocambial cells appear in sequence. If this feature is correct then Sach's canalization mechanism of order arising without a prepattern is unlikely.

A new procambial cell then recruits another epidermal cell so the pattern is one of extensivity or lengthening of the vein (Table 1). Each procambial cell then has one facet attached to an older procambial cell, another facet at the other end of the cellthat does the enlistment and side walls that are inhibited from enlisting procambial cells. This set of differentiated facets then serves as the order by which more cells are added in linear fashion. Spacing is then extensive or invading more area in a sequential manner. Adding new parallel veins in an intercalary manner along with lengthening of veins together create the parallel procambial prepattern.

An even more complex replacement pattern is the branching configuration found in higher plants, moss protonema, fungal hyphae and certain seaweeds There are many types of branching patterns but all seem to involve individual cells. For example, branching in the alga *Cladophora* are outgrowths at the distal end of a cell followed by cytokinesis, that is, an intracellular polarity is present as a prepattern leading to branching as the intercellular pattern (Figure 6A). In seed plants the branching pattern comes from activation of a lateral bud, more specifically, one or more prepattern meristematic cells in a lateral bud.

A fourth type of prepattern-pattern duality is copy where the prepattern remains and is functional as an adaptation. For example watermelon has a pattern of parallel stripes which lie above a set of functional parallel veins. The prepattern for the parallel stripes is then explained as in the earlier example of monocot leaf parallel veins, namely by the presence of procambial cells.

Two speculative mechanisms that might generate prepatterns are the diffusion-reaction system and the gradient concentration concept. The diffusion-reaction system first described by Turing (1952) has two morphogens, one

an activator that diffuses rapidly and the other is an inhibitor that diffuses slowly. One iteration occurs where there is a random deviation of concentrations is introduced followed by many iterations of synthesis and decay of morphogens. Eventually a set of isolated peaks emerges of the activator and some valleys for the inhibitor. The deployment of peaks then serves as a prepattern which are converted into cells that are meristemoids, procambium or eggs. The origin of prepattern order is presence of two morphogens. If the model doesn't work without introducing concentration deviation then the model is artificial. The other possible prepattern mechanism is the diffusion gradient of Wolpert (1969). Here a source cell makes a morphogen and distally a sink cell that absorbs and destroys the morphogen. This system produces a linear concentration gradient over a distance of many cells and cells with different levels of morphogen induce different kinds of cell differentiation. The diffusion- reaction system has yet to be identified in plants but could explain much patternization whereas the diffusion gradient has been discredited by Kerszberg and Wolpert (2006) as too simple to explain pattern formation.

Diffusion is a long-range mechanism for prepatterning. It explains the ordered arrangement of spots on the *Ledebouria* leaf (Figures 4F and G) where nearest neighbor distances ranges from 18 to 33 cells.

A final mechanism for establishing prepattern is cell lineage. Although it seems to have little role in a developing plant (Scheres, 2001) some cases can be found. For example, barb cells along the edge of the elodea leaf are uniformly separated (Figure 5C). Each barb cell and those non-barb cells located basipetally constitute a clone as evinced by all stages of the clone are found in the basal meristem of the leaf (Korn 2008; here Figures 5C and D). It seems that a singular growth center at the tip of a marginal epidermal cell, as in pollen tubes, undergoes mitotic segregation to remain in the most anterior cell of the developing clone. Most likely a cytoplasmic particulate is the prepattern element and the barb cell is the repeating pattern element.

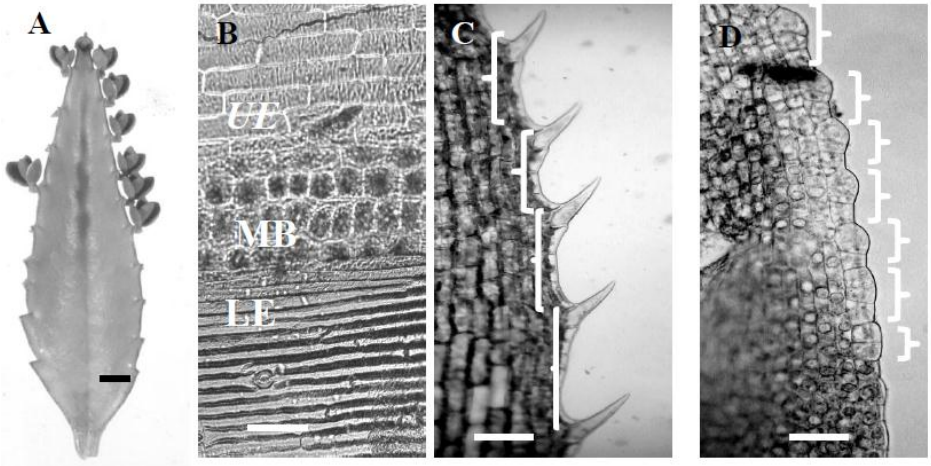

Figure 5. A: *Bryophyllum* leaf with marginal plantlets. Bar is 6 mm. B: Marginal band of *Ledebouris socialis* with isodiametric cells between dorsal and ventral epidermis with stomata. Bar is 400 µm. C: Barb cell clones (left brackets) of mature *Elodea* leaf. Bar is 90 µm. D: Basal meristem region of *Elodea* with various stages of clone formation (right brackets). Bar is 45 µm.

5. Prepatterns and Evo-devo

It is of interest to see if the development in plants and animals have similar prepattern strategies. True et al (1999) found that the locations of melanin areas on the wing of *Drosophila* are determined by veins serving as prepattern. This is similar to sites of the dark green quadrilateral areas on the leaf of *Paphiopedum* as patterns that overlie cross-vein prepatterns. Also in *Drosophila* all cells in an ommitium are precursor cells and each divides into a lineage of about eight cells to form a photoreceptor (Campos-Ortega and Hofbauer, 1978) comparable to epidermal barb cell clones in *Elodea.* The polarized embryo sac originating from a gradient in plants is like the diffusion gradient of the *kno* protein in the *Drosophila* egg. A most curious case in *Drosophila* is the interaction between separate cell lineages of the dorsal and ventral surfaces of the wing disc. The juxtaposition of these two layers forms a margin that is partly responsible for wing growth (Diaz-Benjumea and Cohen, 1993). A parallel case to this is the leaf marginal band between abaxial and adaxial epidermal layers that serves as a prepattern for lateral leaf meristem and pigmented edges (Korn, 2003). While plant and animal evolutions were separated since their independent origins from unicellular forms (Meyerowitz, 2002), it is not surprising that they have discovered similar mechanisms and prepatterns for forming very different structures.

A more relevant comparison is the morphoanatomical similarity of prepatterns in seed plants and the cryptogams. The singular egg in the megagametophyte of gymnosperms and angiosperms has the same status as the egg in the archegonia of mosses and ferns. Its singularity is critical for producing a genetically pure genotype accompanied by surrounding nurse cells. The checkerboard pattern of stomata can also be found in the arrangement of the antheridia of the moss *Funaria hygometricas* (Rajan, 2002, Figure 21.15(a), here Figure 6B) and in the arrangement of archegones in the gametophyte of the fern *Hymenophyllum australe* (Smith 1938, Figure 192, here Figure 6C). The heart-shaped gametophyte of the fern *Thelypteris palustris* is composed of merophytes, clones of cells derived from the sisters of apical cells, and each merophyte produces one marginal papilla (Korn 1993, here Figures.6D -F). Each merophyte is a clone and the potential for the most anterior marginal cell to form a papilla contains a prepattern unit whereas the papilla is the pattern unit. The patterns of *Elodea* barb cells and the fern papillae are similar in occurring within cell lineages, having marginal locations and protruding as protective cell extensions. Similarity, of course, does not prove common descent but all types of prepatterns so far recognized in seed plants have their counterparts in early multicellular forms. If anything, these similarities demonstrate the importance of prepatterns in multicellular development. Dickinson et al (1993) suggested that prepatterns for cuticle morphology in *Drosophila* larvae have been conserved in evolution. Most likely prepatterns in early embryophytes have been conserved through evolution because of their useful role in development. The meaning of homology has been restated by Wagner (1989) to include shared developmental constraints by the same regulatory mechanism which would include those for prepatterning. By this interpretation stomatal and trichome arrangements in the leaf of *Arabidopsis* are homologous patterns as are those for hypocotyl stomata and root hairs.

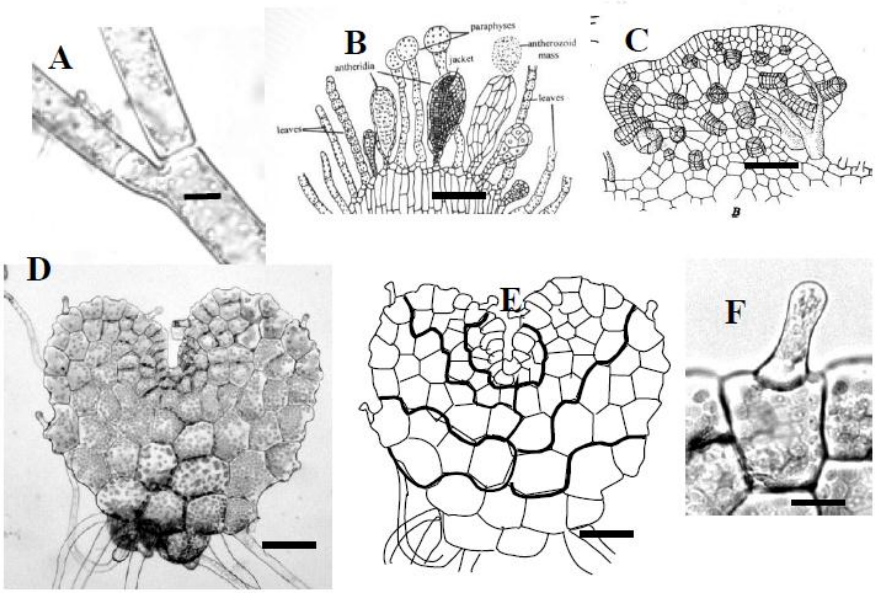

Figure 6. A: Gametophore of the moss *Funaria hygometricas* (Rajan, 2002) Bar is 140 μm. B: Arrangement of archegones in the fern *Hymenophyllum australe* (Smith, 1938). Bar is 80 μm. C: Gametophyte of the fern *Thelypteris palustris.* Bar is 80 μm. D: Same plant highlighting merophytes and papillae. (e) Papilla. Bar is 22 μm.

6. Conclusions

Higher plants explore space, particularly at the organ and organ system levels, in an explosive manner in contrast to animals that have an implosive nature of packing organ systems. These high level structures, such as stems, roots, leaves and reproductive parts do not occur as singular entities but are elements of patterns, such as those of shoots, root networks as well as ovule arrangement, hence, high level structures themselves are elements of higher patterns. For example, the pattern of shoots (stem plus associated leaves) follows a phyllotactic pattern because shoots originate from lateral buds above nodes and node pattern comes from the phyllotactic pattern of leaves.

The first significant idea suggested from prepattern analysis of plant development is its unexpected pervasiveness. Nearly every structure seems to be an element of some pattern in which the pattern comes from a stable prepattern while the elemental structure changes to, or determines, a different, adult structure. Again for example, the particular array of meristemoids in the polka dot pattern remains as the meristemoids developed

into a different, adaptive structure, either stomata, trichomes, glands, or cotton fibers depending upon the background tissue and organ in question.

In animals, Ursprung (1963) suggests that all patterns are derived from prepatterns. His concept of the mechanism has two parts, (a) a prepattern with (b) a background of cells of certain tissue types, the interaction between prepattern elements and background generates a pattern of adult elements. This description is clearly that of Stern (1954) and the one used here. However, Ursprung proposes that all developmental stages are the result of prepatterns that give rise to patterns that, in turn, become prepatterns for later stages, hence there is a trail of prepatterns traceable from the adult all the way back to the fertilized egg (Sondhi, 1963).

That this generalization also holds true for plants is unduly speculative but not necessarily incorrect. It was stated earlier that cases of developmental steps without prepatterns may be because these cases are not understood sufficiently to know whether prepatterns are present or not. Ovule deployment, embryonic formation of the tunica layer and veins *sensu* Sach's canalization are three such cases. If, indeed, these and other cases are found to come from prepatterns, the entire sequence of development can be reduced to a simple strategy of prepattern 6 pattern / prepattern 6 etc. Development is as much a spatial phenomenon as it is one of cell specialization and the spatial aspects are achieved by the appearance of patterns which come from prepatterns which in turn come from spatial ordering in prepattern elements.

It seems that the often used phrase "pattern formation" is actually prepattern formation because pattern is established in prepatterns and simply transferred into pattern by transformation of elements. Much of development of a pattern element is through heterotypic and homotypic inductions, diffusion, cell lineage and possible diffusion-reaction mechanics. These same mechanisms can be found again as prepattern elements that are replaced by pattern elements. Cell proliferation and growth accompany both by providing the fields in which these mechanisms operate.

The second major idea seen from a prepattern perspective is that vascular tissue appears to play an important role as prepatterns. Clear examples of veins serving as prepatterns are cross-veins in determining tessellated pigmentation patches in some orchid leaves and major pedicel veins determining watermelon stripes. Possibly vein activity is the basis of leaf siting (Larson 1975, Korn, 2006b) as well as playing some role in establishing dorsiventrality in leaves (Korn, 2010). Other examples of the role of vasculature in establishing structural patterns are red pigmentation around second order veins in the butterfly plant *Christia orbcordata* 'Striped', in the never-never plant *Ctennanthe oppenheimiana* (Korn, 2010) and the role of vein endings in determining window patterns in *Lithops* spp. (Korn, 2011,). If, indeed, vascular tissue plays a significant role in development as prepatterns then tracheophytes underwent major developmental reorganization during their evolution. The origin of vascular tissue in Tracheophytes is then not only improvement in support and fluid transfer but serving as prepatterns. The pattern of phyllotaxy was described as either by (a) auxin passing against concentration (Mattsson et. al., 2003; Jonsson et al., 2006);Kuhlemeirer, 2007) or (b) branch veins starting a leaf primordium (Larson, 1975; Korn, 2006a). And if it is the latter then veins play the major role in phyllotaxy (Korn, 2010).

The study of plant prepatterns from an anatomical view only sees the "what" and not the molecular "how." Patterns are discovered first then prepatterns followed by genes and then their products. Surveying plants for patterns covers a wide range of taxa whereas patterning genes are usually found in a few model orgasnisms. Consequently the study of plant anatomy remains important in finding new patterns thereby making anatomy more than simply the syudy of structure but also includes the search for the origin of order in structure.

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