

On the classification of meristems

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Summary: Various principles of the classification of meristems are critically examined. A more consistent genetic classification of meristems is proposed.

Keywords: meristem, promeristem, semimeristem, eumeristem, massive meristem, plate meristem, rib meristem, procambium, cambium, phellogen, apical meristem, lateral meristem, diffuse meristem, marginal meristem

The meristems have repeatedly been scrutinized due to their paramount role in growth and morphogenesis of plants. Vast academic and scientific literature covers these processes. However, the lack of precise terminology for describing the meristems greatly complicates the perception of this literature. This article aims to revise the widely used classifications of the meristems, to standardize terminology for their description and to elaborate a more consistent meristem classification.

Unlike the animal development, “the development of plants is morphologically an increment (‘adding’) of one unit above another” (TAKHTAJAN 1954: 70). The addition of every unit is associated with a drastic morphological and functional change of previously arisen units caused by metamorphosis and differentiation of their constituent cells (RADKEVICH 1947).

Any cell of a higher plant goes through 3 developmental stages, viz. embryonic, elongation and differentiation stage. In the latter one, some morphological specificities form in the cell which cause its transformation into the component of a certain permanent tissue. This transformation is associated with a gradual ceasing of cell divisions up to a complete loss of the cell’s ability to divide. Each living cell of a higher plant is capable of dedifferentiation and reversion to nearly embryonic state. However, such a reversion is usually hampered by correlative factors that limit the development of the cell according to its location in the organ. Therefore, some special cells are needed that retain the ability to divide for a long period of time in order to maintain long-term plant growth. Assemblages of division-capable cells located in specific parts of the plant’s body, constitute the generating tissues also called meristems.

The meristems are arranged according to the polarity laws. The longitudinal polarity is expressed in the appearance of the apical and basal growing zones as early as in plant embryo. These zones maintain the growth in length and lateral branching of the shoot and root. Thickening of the axial organs takes place at later developmental stages and results from the radial polarity (SINNOTT 1960; KAUSSMANN 1963; GUTTENBERG 1965; BLOCH 1965; WARDLAW 1965).

The polarity is primarily due to the ability of meristem cells to unequal differential divisions. Only one of the daughter cells remains genuine meristematic. Another daughter cell additionally

¹ Upgraded version of LOTOVA (1977)

divides once or twice to give rise to the cells which begin to differentiate (BÜNNING 1965; BLOCH 1965). Continuous activity of a meristem does not lead to the aging of its cells, because every cell division in it produces a pair of developmentally young sister cells that replace the mother one. That is why NEWMAN (1965) considered the meristem tissue as successive generations of cells.

The meristem cells are routinely reported to have typically a large nucleus, usually several nucleoli, a poorly developed vacuolar system, evenly thin cell walls and the absence of reserve substances. The meristem cells also have proplastids, promitochondria and golgiosomes; the size and number of these organelles depend on the activity of the cell. ER structure is most labile. It is usually underdeveloped and looks like separate cisterns and short tubules (BOUREAU 1954; WHALEY et al. 1960; ESAU 1963; ROSTOVTSSEVA 1969). The above-listed features are mainly inherent in the cells of so-called eumeristem (*sensu* KAPLAN 1937), which takes the greatest part of the shoot apex. Cells of other meristem types can differ from eumeristem cells in different ways. For instance, meristematic cells of the plant embryo are filled with reserve nutrients. The usually tetrahedral apical cell in the shoot and root of pteridophytes is rather vacuolated (POPHAM 1951), and so are the procambial and cambial cells. The cell walls of the central mother cells of the shoot apical meristem are unevenly thickened like the cell walls of the angular collenchymas (FOSTER 1938; POPHAM 1951). Radial cell walls of the cambial cells are much thicker than the tangential ones, especially in winter (LOTOVA 1959; KAUSSMANN 1963).

Thus, there are no reliable morphological criteria to distinguish the meristem cells from differentiating ones or even from some completely differentiated cells of a permanent tissue. Hence, the applicability of the term 'meristem' should be clarified. Whether only groups of actively dividing cells located in a certain part of the plant body should be called 'meristem' or this term could be extended to the partly differentiated, but still dividing cells adjacent to these groups (NEWMAN 1965)?

EAMES & MACDANIELS (1947) discriminated the concepts of 'meristem' and 'meristematic cell'. They termed 'meristems' only the tissues that are strictly localized in the plant body and perform a morphogenetic and/or histogenic function while 'meristematic cells' are scattered throughout the plant body, as they are any living cells which have regained mitotic divisions. SACHS (1874) attributed such cells to the 'old' meristem (Altmeristeme).

Synopsis of the meristems in higher plants (Fig. 1) was published by LOTOVA (1977), but the meristems are usually classified separately according to their morphological or functional and physiological or topographical or genetic characteristics (SACHS 1874; LINSBAUER 1916; SCHÜEPP 1926; EAMES & MACDANIELS 1947; RAZDORSKY 1949; KAUSSMANN 1963; KARAGYOZOVA 1965 etc.).

Morphological classification

The root and shoot apices are occupied by eumeristems typically consisting of isodiametric polyhedral 'parenchymal' cells (BLOCH 1965). Division of these cells and the elongation of their derivatives result in the prosenchymal cells typical of procambium and cambium.

The meristems of 'parenchymal' cells are usually classified into 3 groups according to the directions of their cell divisions (SCHÜEPP 1926; EAMES & MACDANIELS 1947; BOUREAU 1954; KAUSSMANN 1963).

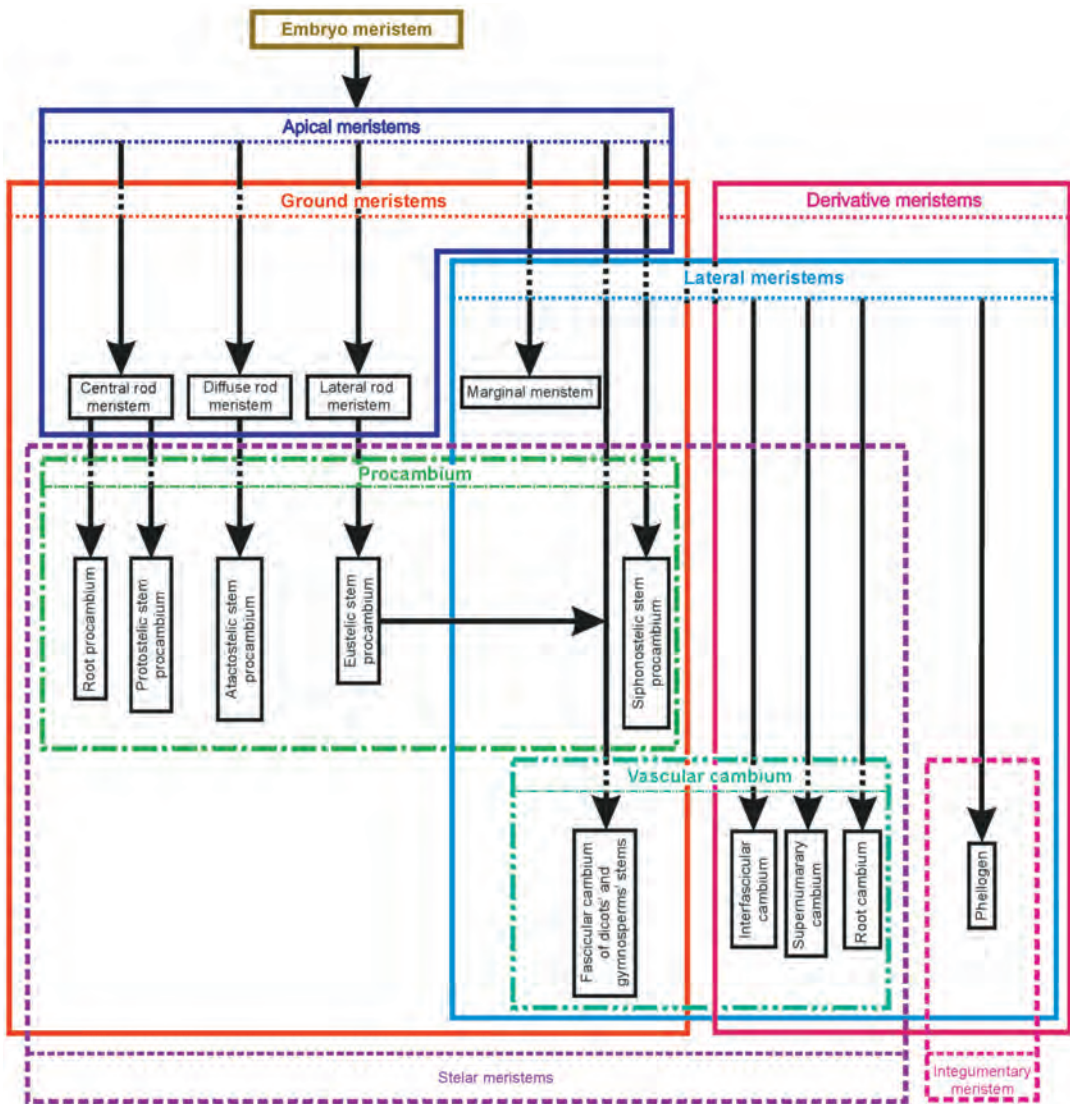


Figure 1. Types of the meristems of higher plants and their interrelationships.

1. The massive (block) meristems (Massenmeristeme, massige Meristeme, Blockmeristeme) are characterized by variously directed 3D cell divisions which result in a volumetric growth of an organ. These meristems produce, among other things, moss antheridia, sporangia of the eusporangiate ferns or endosperms of seed plants.
2. The plate meristems (Plattenmeristeme) consist of cells which divide 2D to maintain plane extension of an organ/tissue. 2D anticlinal cell divisions give rise to the epidermis as well as to the inner tissues of the developing leaf. The phellogen can also be assigned to the plate meristem due to unidirectional divisions of its cells.
3. The rib meristems (Rippenmeristeme, file meristems) are composed of cells dividing mostly transversely. Therefore, they are represented by lengthwise cell rows in the longitudinal section of an organ, as the meristem of monocot root tip or the medullary meristem of the shoot apex of seed plants (POPHAM 1951; BUVAT 1955).

Topographic classification

The topographical classification of meristems is based on their position in the plant body (EAMES & MACDANIELS 1925, 1947; RAZDORSKY 1949; YATSENKO-KHMELEVSKY 1961; ROMBERGER 1963; KAUSSMANN 1963; ZHUKOVSKY 1964; ESAU 1965a; KARAGYOZOVA 1965; KURSANOV et al. 1966; STRASBURGER et al. 1971).

1. The apical meristems are in the apices of shoots and roots; they maintain lengthening of these organs. The shoot apical meristem is also involved in formation of the leaf primordia and axillary buds. The apical root meristem is only histogenic, since it does not produce any lateral organ. Lateral roots are initiated in the pericycle of older parts of the parent root, where conductive tissues are already differentiated. The apical meristems can additionally arise in any organ and in almost any topographic zone of the organ by means of meristemization of permanent tissue cells. Such meristems are initial developmental stages of adventitious roots or shoots, respectively. They are physiologically equivalent to the apical meristems, but are quite different in their origin and position in the plant body.

2. The lateral meristems carry out axial organ thickening. Examples for these meristems are cambium and phellogen. The procambium is also commonly referred to as lateral meristem. However, the procambium as a lateral meristem is only characteristic of the siphonostelic stems of most ferns. The procambium can be attributed to the central rib meristem in the protostelic stems of archegoniate plants and all roots. It could be classified as diffuse rib meristem in the stems of monocotyledons. BLOCH (1965) proposed the term 'mosaic procambium' for denoting procambium in the stems of monocotyledons. Procambium initiates as a series of separate strands in young eustelic stems of gymnosperms and angiosperms. In woody plants and some herbs, these strands subsequently merge and form a ring intersected by narrow rays in cross-sectioned stems. Such a procambium would better being assigned to the lateral rib meristem.

3. The intercalary meristems are in the internodes and basal parts of the leaf axes at the very beginning of their development. These meristems are traditionally attributed to the basalmost parts of lengthening internodes and linear leaf blades, especially those in grasses, and to the distalmost parts of lengthening petioles. Such an attribution is irrelevant; it arose from the confusion between the concepts of 'intercalary meristem' and 'intercalary growth', although the latter could be performed without cell divisions (EAMES & MACDANIELS 1925; ESAU 1965b). Not meristems, but differently developed permanent tissues are in the listed parts; the conductive tissues are even functioning. The tracheary elements of the protoxylem develop annular or spiral lignified secondary cell walls there.

PRIESTLY (1928) attributed the cambium and phellogen to the intercalary meristems, because their functioning resembles the intercalary growth in that new cells of the permanent tissues are produced between the previously formed cells.

4. Diffuse meristem is scattered through the plant body. This meristem is most expressed in algae and fungi. Each cell of their thalli is capable of dividing to maintain thallus growing. However, most algae and fungi have no genuine tissues. Accordingly, the concept of diffuse meristem is hardly applicable to these living beings. In higher plants, the intercalary meristem is the most similar one to the diffuse meristem.

5. The marginal meristem is in the developing leaf primordia of some plants. It gives rise to the lamina except for the midrib.

The topographical classification of meristems is most popular among botanists. However, the given examples clearly show that this classification is rather conventional. It needs greater accuracy and further elaboration of issues concerning the position of the procambium therein.

Genetic classification

The genetic classification of the meristems based on their origin is even more controversial. These meristems are usually categorized into the promeristem, the primary meristem and the derivative (= secondary) meristem (EAMES & MACDANIELS 1925; RAZDORSKY 1949, 1955; BUVAT 1965; KURSANOV et al. 1966). However, there are no standardized criteria for delimiting these meristem types. So, the term 'promeristem' is used most arbitrary (SUSSEX & STEEVES 1967).

The term 'promeristem' is usually applied to undifferentiated cells which make up either the whole apical meristem (= eumeristem) (EAMES & MACDANIELS 1925; ALEXANDROV 1966) or only the most terminal cell layers of the apex (SACHS 1874; CLOWES 1961; KURSANOV et al. 1966). ESAU (1954) considered the promeristem as consisting of the most actively dividing initial cells and their derivatives. LINSBAUER (1916) called the initial cells 'archimeristem', whereas NEWMAN (1956, 1965) termed them 'apical cells'. These cells can be rather similar to other meristem cells in shape and position in the apex. NEWMAN (l.c.) recognized two modes of replenishment of the apical cell pool. The first mode are intense divisions of the apical initial cells while their derivatives gradually move away from the shoot tip, cease dividing and differentiate into the elements of permanent tissues. The second mode are rare divisions of the apical initial cells, but intense divisions of their derivatives which constitute a so-called 'general meristem'.

BHAMBIE (1972) termed the apical meristems of roots and shoots of pteridophytes 'indeterminate', as they remain active for a long time. KORCHAGINA (1975) stressed the tendency to name 'indeterminate' only the initial cells which are able to self-perpetuating and give rise to the more determinate meristems constituting different zones of the shoot apex (flank meristem, rib meristem, zone of the central mother cells etc.) (FOSTER 1938; POPHAM 1951; GUTTENBERG 1960).

KRASHENINNIKOV (1937), POPOV & POPOVA (1964) considered the promeristems to be descendants of the embryonic meristem, the latter one being attributed to the primary meristems by BUVAT (1965) later on. EAMES & MACDANIELS (1925) considered the promeristem the initial developmental stage of the primary meristem. ALEXANDROV (1966) classified the promeristem as the primary one, but KRASHENINNIKOV (1937), BORODIN (1938), KRAMER & KOZŁOWSKI (1960) referred to the whole shoot apical meristem as the primary one. SINNOTT (1960) termed the whole shoot apical meristem primary meristem. YATSENKO-KHMELEVSKY (1961) did not associate the term 'promeristem' with the origin of other meristem types; he suggested using it as exclusively descriptive.

The promeristem derivatives develop into partially differentiated 'meristems' in the subapical zone of the shoot. Mitotic activity of their cells is lower than that of the apical meristematic zone. These 'meristems' of less frequently dividing cells were called by SACHS (1874) semi-meristematic tissues (= 'deuteromeristems'). HABERLANDT (1924) coined the terms 'protoderm', 'ground

meristem' and 'procambium' to refer to these tissues. The protoderm was originally thought to consist of few cell layers. However, this term is usually applied nowadays only to the superficial cell layer which changes into the epidermis (ESAU 1965a,b). HABERLANDT (l.c.) considered the term 'procambium' as collective to refer to any more or less prosenchymal semimeristematic cells that differ in their shape from the cells of the ground meristem. So, he applied this term for designating semimeristematic cells which generate not only the conductive tissues but also the sclerenchyma and even parenchyma. German plant anatomists (GUTTENBERG 1965; KALBE 1962) often categorized the ground meristem into 'Phloeogen' and 'Myelogen' which give rise to the cortical and pith tissues, respectively.

Recognition of these three semimeristems generally corresponds to the developing anatomical-topographic zones of the stem: the most peripheral, prospective cortex, prospective pith and small-celled meristematic zone in between the latter two. This zone looks like a ring in the stem cross section and it was described by SANIO (1863) as a 'thickening ring'. KOSTYTSCHEW (1920) proposed to rename this zone 'procambial ring', although he pointed out the inaccuracy of this term, because this zone becomes clearly discernible in the shoot apex before the development of the genuine procambium of long narrow cells.

Development of the conductive system in the seed plant stems is greatly influenced by the developing leaves. Accordingly, the procambium, as the vascular semimeristem, originates nearby the bases of early leaf primordia (ESAU 1954). The ground meristem cells there divide longitudinally in different planes and their derivatives elongate to change into prosenchymal cells typical of the procambium. The procambium induces new cell divisions in the ground meristem, incorporates them and expands bi-directionally from the initiation sites as one or several strands outwards into the leaf and inwards to the semimeristematic ring in the stem (ESAU 1943). It spreads downwards the stem in this semimeristematic ring.

Developing procambium takes up the total width of the semimeristematic ring or only its inner part, while leaving its outer cells to transform into pericyclic parenchyma/sclerenchyma. The cells of the semimeristematic ring between the procambium strands give rise to the primary ray parenchyma. These rays are very narrow, often uniseriate in woody plants, but rather wide in most herbaceous ones. The ray cells are able to generate an interfascicular cambium in many plants.

Thus, the semimeristematic ring performs a histogenic function. It generates the vascular semimeristem and some permanent tissues. Therefrom, BARANETZKY (1901) suggested to term this semimeristem the 'generating ring'. KONDRATIEVA-MELVILLE (1956) tried to revive BARANETZKY's term instead of 'desmogene', 'prodesmogene', 'provascular meristem', 'prestelar tissue', 'provascular tissue', 'residual meristem', etc. (ESAU 1965). Her position is somewhat incorrect, since each of the above mentioned terms reflects one of the specifics of this semimeristematic ring. The term 'generating ring' characterizes this semimeristem as the place, where the procambium initiates in the stem, but neither its structure nor its origin. Therefore, the semimeristem of the generating ring can relevantly be considered as the residual (semi)meristem associated genetically with the shoot apical (true) meristem.

As to the angiosperms, the generating ring was detected only in dicotyledons except for the plants with very narrow apices (ESAU 1943). This structure is indiscernible in the monocotyledons. Therefore, the procambium differentiates directly from the ground meristem in the latter.

The shoot apical meristem and its derivative protoderm, ground meristem and generating ring meristem can all be attributed to the primary meristems. However, the procambium and its derivative cambium are still to be decisively attributed either to the primary meristems or to the secondary ones.

ROTHERT (1897) thought the secondary meristems to arise in rather old plant organs without any connection with the apical meristem. Accordingly, neither procambium nor cambium can be considered the secondary meristem, because both descend from the residual meristem which is a continuation of the apical meristem.

KRASHENINNIKOV (1937) believed that the secondary meristems develop from the primary ones or from the permanent tissues, but he considered the procambium as the primary meristem, though it arose from the (primary) apical meristem. On the contrary, BORODIN (1938) classified the procambium as the secondary meristem, because it formed from the ground meristem or residual meristem. Such an equivocal attribution of the procambium to the primary or secondary meristems results in the same equivocal attribution of the cambium.

EAMES & MACDANIELS (1925), GUTTENBERG (1965), ALEXANDROV (1966), KRAMER & KOZŁOWSKI (1960), STRASBURGER et al. (1971) classified the cambium as the primary meristem, because they interpreted it as a continuation of the procambial cell layer which remained meristematic. BORODIN (1938) also considered that the cambium and procambium differ only in the directions of their cell divisions. RAZDORSKY (1955) pointed out that procambium modified into the cambium. Therefore, it is often considered a secondary meristem (GENKEL & KUDRYASHOV 1964; KURSANOV et al. 1966; BARYKINA et al. 1971). The secondary nature of the vascular cambium could be confirmed by the so-called supernumerary cambia which cause the so-called anomalous secondary thickening in many centrosperms, some lianas, cycads, gnetums, etc. (PFEIFFER 1926; ILJIN 1950) and which arise in the cortical or pericyclic parenchyma. The supernumerary cambia are reasonably attributed to the secondary meristems. However, they are certainly non-homologous with the typical vascular cambium.

The secondary nature of the vascular cambium is usually proved by radial arrangement of the cells in the cambial zone, dimorphism of the cambium cells (fusiform and ray initials) and mostly tangential cell divisions, all the traits distinguishing it from the procambium. These differences are actually rather nominal (ESAU 1954).

The cells are also row-arranged in the certainly primary rib meristem and the cambium-like zone of the seed plant shoot apex (POPHAM 1951). Radial rowed arrangement of the procambial cells is reported to be inherent in tobacco plants (ESAU 1965b). Like the cambium, the procambium in stem of *Apocynum sibiricum* consists of fusiform and ray initials (CUMBIE 1963). Small time gaps are observed between the appearance of procambium and cambium in most plants. The latter often develops before the primary conductive tissues complete their differentiation (KOSTYTSCHEW 1920; KONDRATIEVA-MELVILLE 1956). Furthermore, the procambium and cambium are difficult to be distinguished by their derivatives. Thus, the procambium-produced conductive elements of the monocotyledonous plants are as advanced as the cambium-produced ones of the dicotyledonous plants. The vascular cambium of dicotyledonous creepers usually forms extensible xylem elements similar with those formed by the procambium (PHILIPSON & WARD 1965).

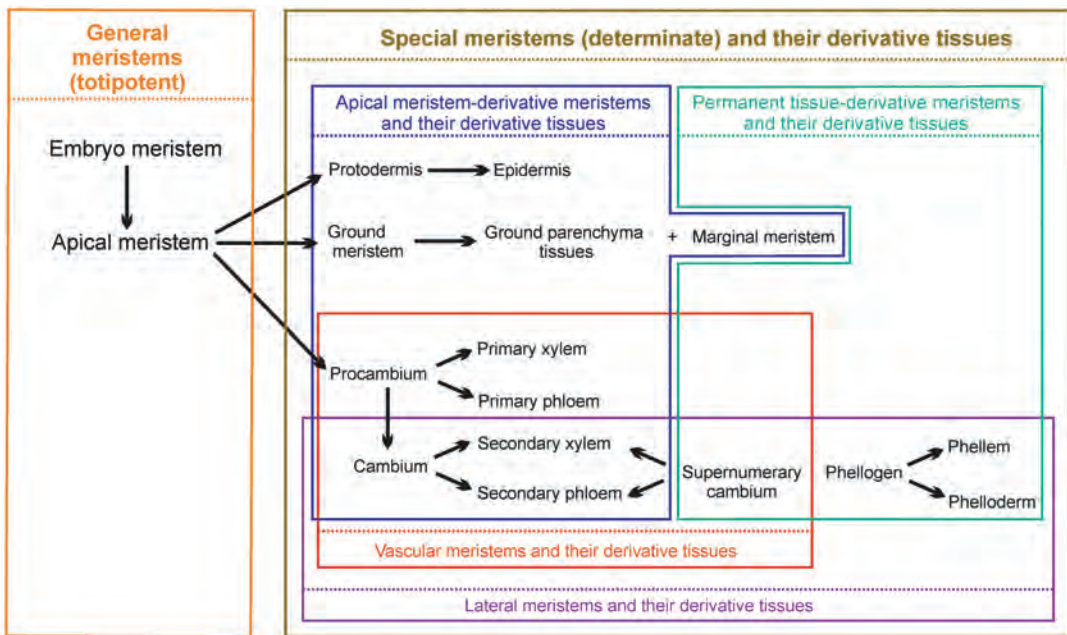


Figure 2. Suggested meristem classification.

ESAU (1943, 1954, 1965a,b) used these data as argument for recognizing procambium and cambium as different developmental stages of the same meristem and not as serial different meristems. This meristem remains at the first developmental stage in monocotyledons and pteridophytes, but it passes to the second developmental stage in dicotyledons and gymnosperms.

BORISOVSKAJA (1965) disputed this conclusion, as she thought that the vascular cambium had more intense cell divisions resulting from the age-related changes in plant organs.

YATSENKO-KHMELEVSKY (1961) believed that the vascular cambium had arisen as a typical secondary meristem differentiating in the parenchyma without any relation to the procambium. In more advanced plants, it becomes a derivative of the procambium. The vascular cambium in roots seems to be still of secondary nature, because it originates from the incompletely differentiated parenchyma cells near the phloem strands (RAZDORSKY 1949, 1955; POPOV & POPOVA 1964).

The opposition of the primary and secondary meristems is arbitrary as clearly evidenced by the thickening mode of monocotyledons' stems. The primary thickening meristem differentiates nearby the shoot apex in these plants. Its cells are in radial rows. Activity of this meristem results in lifting leaf primordia above the apex in many plants, especially in palms. In some 'woody' monocotyledons, this meristem continues and produces vascular bundles without protoxylem (ESAU 1943; ILJIN 1950; KAUSSMANN 1963). Therefore, these bundles and the meristem they originate from are considered secondary. In other words, the primary thickening meristem continues as the secondary thickening meristem.

Contradistinction of primary and secondary meristems seems to have resulted from the opposition of the primary and secondary permanent tissues (ESAU 1954). The latter are permissibly distinguished only in the sense that one permanent tissue precedes the other. The primary tissues develop during the period of apical lengthening of an axial organ. The secondary tissues

differentiate after the apical lengthening has ceased and organ thickening has begun (ESAU 1965a). However, an axial organ attains its anatomy continuously and the secondary thickening usually begins before the primary tissues complete developing. For this reason, contrasting the primary, secondary and even tertiary (VAN THIEGHEM 1891; ZHUKOVSKY 1957) meristems seems morphologically unacceptable.

LINSBAUER (1916) reasonably operated on the concepts of progressive and regressive meristems instead of conventional primary and secondary ones. The progressive meristems gradually progress, starting with the apical meristem. The vascular cambium in stems of seed plants would exemplify the progressive meristems. The regressive meristems, as exemplified by the supernumerary cambium and phellogen, arise in the full-developed organ parts by means of cell dedifferentiation in the permanent tissues. LINSBAUER considered formation of the regressive meristems similar to the regeneration process.

Conclusion

Thus, many shortcomings are in meristem classifications.

- The morphological classification which is based on the directions of cell divisions is applicable only to the meristems of isodiametric cells.
- The topographic classification ignores the different position of the procambium which determines stele type in an axial organ, and it also neglects the procambium in leaves.
- The genetic classification disputably discriminates the primary and secondary meristems.

In this regard, I propose to classify meristems according to their interrelations and relations with their derivative tissues (Fig. 2). The general meristems are indeterminate, i.e. totipotent. They are able to generate any permanent tissue of an organ. The special meristems are determinate in the sense that they produce only some permanent tissues or even only one tissue. These meristems come from either an other meristem/semimeristem or from the permanent tissue. I hope this classification would be some advance to a more comprehensive insight into the meristem diversity.

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