

Proceedings of the Iowa Academy of Science

Volume 14 | Annual Issue

Article 8

1907

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Henry S. Conard

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Recommended Citation

Conard, Henry S. (1907) "Homology of Tissues of Ferns," *Proceedings of the Iowa Academy of Science*, 14(1), 85-87.

Available at: <https://scholarworks.uni.edu/pias/vol14/iss1/8>

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HOMOLOGY OF TISSUES IN FERNS.

BY HENRY S. CONARD.

In comparing two or more organisms our standpoint may be developmental, morphological or physiological. Or, we may strike a middle ground in what is called the morpho-physiological point of view.

Morphology and development agree in using the word *homology* to designate the relation between two organs which have a similar origin in the development of the individual, i. e., in ontogeny. For such organs we freely assume a common phylogenetic origin. An example of this is the relation of the spore mother cell of a moss to the pollen-spore mother cell of a flowering plant. They are homologous organs. Purely physiological similarities are termed by common consent *analogies*. The relation between a tendril of a pea and that of the grape is only analogy. One is a modified leaflet, the other a modified shoot. The two organs have nothing in common either in ontogeny or phylogeny, save the common irritability of their living substance.

In all of the higher plants, however, there is continual new growth of organs from embryonic or meristem tissues. Thus a kind of serial homology is found, similar parts being successively formed anew in the growing regions. In such cases we find that the morpho-physiological basis of comparison is the truer one, and leads to sound phylogenetic conclusions. It is my intention to demonstrate this by reference to the structure and development of fern-plants (Pteridophytes).

First we shall see that similarity or difference in the origin of tissues from the apical cell or primitive meristem (*Urmeristem* of Haberlandt) is, in many instances, of no significance. It is well known that the roots, stems and leaves of ferns are traversed by continuous vascular tissues which serve to convey and distribute the sap, and that the details of these tissues are similar in whatever organ they are found. The endodermis, phloem and xylem are perfectly distinct and homogeneous tissues. The epidermis also is, in most ferns, a continuous tissue all over the exterior of the plant. Only at the growing points are these tissue relations interrupted.

Are these tissues homologous throughout the various organs of the individual and in different individuals and species?

Every cell of the root takes its origin from a single apical cell which is shaped like a three-sided pyramid, and cuts off segments on all four faces. Every cell of the stem originates from a similar apical initial which cuts off segments on three faces. The young leaf has for a time a similar tetrahedral initial with three planes of division, then the initial becomes "two-sided," and after the rudiments of eight to eleven pinnae are established (in *Dennstaedtia punctilobula*) the single initial is replaced by a group of apical initials of equal rank. Therefore, since each organ has its own type of initial, or may have several types in the course of its development, it is plain that the relation of a given tissue, the xylem for example, to the apical cell cannot form a final basis of homology.

However, the apical cell or cells do not give rise at once to permanent tissues. They form rather an embryonic tissue, the primary meristem of Haberlandt, out of which the permanent tissues are gradually moulded. Now, in the leaf of *Dennstaedtia punctilobula* (Boulder Fern; Hay-scented Fern) the primary meristem may come from a two-sided initial, or from a group of marginal initials. Similarly, in the stems of true ferns (Filices), Marattiaceae and Cycads primary meristems arise from a single tetrahedral cell, or from a group of initials. But as no one questions the close phyletic relationship of these three groups, neither can we question the essential homology of their primary meristems. The origin of the primary meristems, therefore, need not figure in our discussion.

Can we draw any inferences, then, from the manner in which mature tissues arise from this primary meristem? Hanstein long ago observed in certain flowering plants an early division of the meristem into three concentric zones: (1) the plerome or central portion which gives rise to the pith and vascular tissues; (2) the periblem surrounding this, which gives rise to the cortex of the mature stem; and (3) the dermatogen on the outside, which is the embryonic epidermis. The division between plerome and periblem falls just inside the endodermis. A similar alignment of cells in the primary meristem occurs in the roots of ferns (Filices). But the line of division is different in stems and leaves of ferns (at least in *Dennstaedtia punctilobula*), where the endodermis is the outermost layer of plerome. Must we, then, believe that the endodermis of roots is not homologous with that of the stem and leaves of the self-same plant? I cannot so believe. But it is on such

morphological grounds that Campbell (Mosses and Ferns, 1905, p. 465) denies the homology of the vascular system of *Equisetum* with the central vascular strand of *Sphenophyllum*. He says of *Equisetum*, "the whole vascular system of the stem originates from the primary cortex or periblem, the original central tissue-cylinder giving rise only to the pith." The same arguments would apply in comparing the stems of *Lygodium* and *Adiantum*, or the very young and the mature individual of *Dennstaedtia*. That the vascular tissues of the individual fern are serially homologous follows from the observed facts of development. That they are phylogenetically homologous in different individuals and different species is indicated by the exact parallelism, pointed out first by Jeffrey and Boodle, between the ontogenetic and phylogenetic series. Hence any negative argument based on the origin of tissues in primary meristem must fall. The developmental viewpoint is manifestly a guide to phyletic relationship.

Shall we then be free to adopt the purely morphological basis, and consider similarity of structure equivalent to community of origin? By no means. The single initial cell of the moss (*Musci*) sporophyte, for example, has no direct relation to that of *Equisetum* or the leptosporangiate ferns. For if we can think of any ancestor of the pteridophytes among the byrophytes, it must be in the *Hepaticae* and not the *Musci*. But no living hepatic shows any well marked apical growth in the sporophyte. Therefore it is most probable that growth by a single initial has arisen independently in mosses and ferns. Again, in true ferns the cortical and medullary tissues often show striking resemblances. But ontogeny teaches us that they have very different histories. They may be truly considered as a unit, the fundamental tissue. But the parenchyma enclosed by the vascular ring is no more to be called cortex than is that outside to be called medulla. Hence a strict morphological basis of homology is not tenable.

So we must come back finally to the conclusions which follow at once from morpho-physiological considerations. Those tissues are homologous whose form, function and position in the organism point to a common origin. And we may safely say that the normal primary vascular tissues of all vascular plants are truly homologous.