Some "Atypical" Stem Structures in the Gramineae

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Abstract

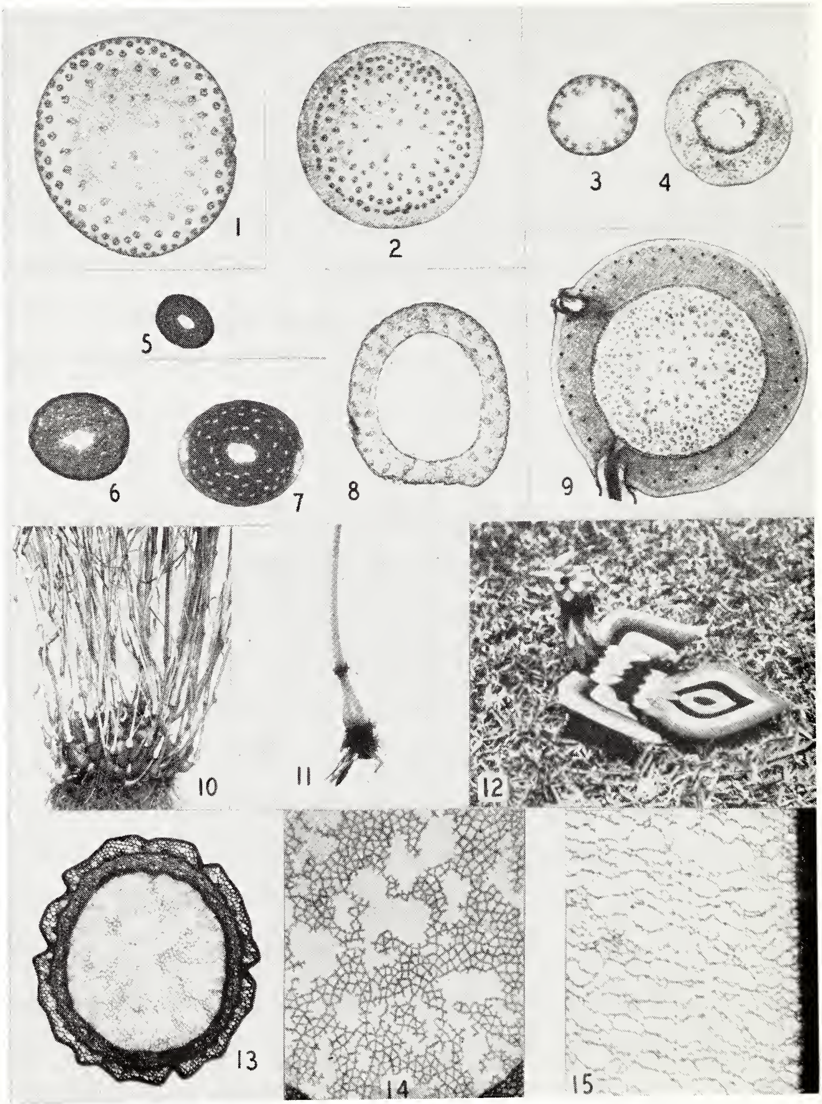
To regard the stems of such grasses as wheat or corn as "typical" of the Gramineae is to overlook some interesting and significant deviations in vascular and parenchymatous pattern. Some of these, occurring in the culms and rhizomes of representatives of such genera as *Andropogon, Olyra, Zizaniopsis, Arrhenatherum, Phleum, Melica, Cinna,* and *Hymenachne,* are pointed out and described.

Many of the brief general descriptions of the grass family, such as those given in encyclopedias or as introductions to taxonomic treatises, cite the hollow stems of such plants as wheat, rye, or bamboo as "typical" for the family. It is true that they usually mention the solid stems of corn or sugar cane, but in stressing the mechanical advantages of the hollow one they often leave the impression that the solid one is of rare occurrence. This treatment does not do full justice to the solid stem, and it overlooks some interesting deviations from these two types.

Formation of the hollow internode can easily be traced downward from the apical meristem. The young internode is solid, but the provascular strands appear only in the outer part. As the internode grows older and elongates, the cells of the peripheral region continue to divide, and some of them elongate, this activity finally being limited to the intercalary meristem at the lower end of the internode. However, the parenchyma cells in the middle soon cease to divide, but grow larger, become highly vacuolate, are finally torn apart by the elongating action, and ultimately disintegrate. Maturation of the vascular tissues and fibers, often accompanied by extensive lignification of parenchyma cells, forms a firm outer layer, giving to the internode its characteristic rigidity and strength. The inner wall of the hollow cylinder thus formed usually bears a few ragged remnants of the parenchyma cells destroyed in the process.

The solid type of stem, that is, the one in which the body of the fully developed internode is completely filled with tissue, is to be found in one or more species of probably one-fifth of the 500 or more genera now recognized by systematists. In most of these the vascular bundles are scattered over the cross section of the internode, as in the well-known corn stem, being larger and more widely spaced in the middle of the section. Since this type of stem is found in some members of the Bambuseae and in most, if not all, of the Maydeae, thus at opposite ends of the phylogenetic spectrum, it would seem to have little evolutionary significance.

Between the hollow and solid forms there is an intermediate condition in which the middle of the internode is devoid of vascular tissue and the parenchyma breaks down irregularly, leaving a ragged lacuna which may vary in size and shape in different specimens of a species or even in different parts of a single individual. An interesting variation of



FIGURES 1, 2. *Culm and rhizome of* Euchlaena perennis.

FIGURES 3, 4. *Culm and rhizome of* Agropyron repens.

FIGURES 5, 6, 7. *Culm, rhizome, and stolon of* Cynodon dactylon.

FIGURES 8, 9. *Culm and rhizome of* Zizaniopsis miliacea.

FIGURE 10. *Clustered corms of* Arrhenatherum.

FIGURE 11. *Corm of* Cinna.

FIGURE 12. *Ornamental bird, made from dyed parenchyma cores of* Hymenachne.

FIGURE 13. *Section of stem of* Hymenachne pseudointerrupta.

FIGURES 14, 15. *Transverse and longitudinal sections of stem parenchyma of* Hymenachne.

this type was reported many years ago in a South American species of *Olyra*. In it the central part of the parenchyma of the internode disintegrates, leaving one or usually more vascular bundles free, extending from node to node in the cavity (6).

Whatever the structure of the culm may be, we usually find a very different picture on examining the rhizome or stolon of the same plant if it has either of these structures. Although the internode of the upright stem may be hollow, there is a strong tendency for that of the horizontal structure, especially the rhizome, to have a solid pith. And, while the vascular bundles of the culm tend to be concentrated toward the periphery, the horizontal structures usually show a more or less definite cortical region having few or no vascular bundles.

One of the simplest illustrations of this difference between culm and rhizome may be seen in the perennial teosinte plant, *Euchlaena perennis* Hitchc. The culm of this grass is so much like a corn stem in structural pattern that the two are almost indistinguishable (Fig. 1). But if a series of cross sections are cut, one from each internode, continuing downward as the vertical stem becomes a horizontal rhizome, a progressively widening cortical zone is seen (Fig. 2). The common weed, *Sorghum halepense* (L.) Pers. (Johnson grass) has the same structure, but with a more variable expression. In this species, vertical rhizomes, which often grow to considerable depth in porous soils, also show this cortical region.

The well known quack grass, *Agropyron repens* (L.) Beauv., is fairly representative of a large number of species in which, although the internodes of both culm and rhizome are hollow, the rhizome tends toward the solid form (Figs. 3, 4). The vascular bundles of the culm are arranged in circles toward the outside, the outer circle consisting of very small bundles set in a ring of sclerenchyma just beneath the epidermis. Although the rhizome may have a diameter at least twice that of the culm, its lacuna is much smaller than that of the culm. Here the main vascular bundles are located in a ring of sclerenchyma which has a diameter about half that of the rhizome. The cortical region consists mostly of parenchyma with a few vascular bundles which come in from the leaves and will enter the central cylinder at a morphologically lower level.

Some species such as Bermuda grass, *Cynodon dactylon* (L.) Pers., have both rhizomes and stolons, the latter usually standing somewhere between the culm and the rhizome in structure (Figs. 5-7).

A much more striking difference between culm and rhizome is found in the aquatic grass, *Zizaniopsis miliacea* (Michx.) Doell. & Aschers. The culm internode is hollow and not very different from that of other hollow stems (Fig. 8). But a cross section of the rhizome (Fig. 9) shows a clearly defined cortical region set off from the central cylinder by a row of cells having much the appearance of an endodermis. Thus far, however, tests have failed to show any suberization of the cell walls of this layer. The central pith is solid, with vascular bundles scattered over it much as in the corn stem. The cortical region has many rudimentary vascular bundles, some of them consisting merely of strands of fibers. Adventitious roots arising from the rhizome have their origin in the outer part of the central cylinder, giving to the cross section much the appearance of a section of a root at the place where a branch root arises.

These marked differences between culm and rhizome lead us to ask what factors cause the apical meristem to leave behind it one pattern of structure when moving horizontally to form the one and then to change the pattern as it turns upward to form the other. The difference cannot be wholly due to the horizontal position of the one structure and the vertical position of the other, because in some species, such as *Sorghum halepense,* segments of rhizomes in both positions are alike in structure. Neither can it be attributed wholly to the underground as opposed to the aerial environment since stolons show much the same pattern as rhizomes. The answer to the question must lie somewhere in that relatively unexplored region between the extensive studies on tunica and corpus on the one hand and what is known of the gross morphology of the mature stem on the other.

Another deviation from what is regarded as the typical stem structure is the formation of bulb-like swellings in the basal internodes of culms. Frequently only one internode is involved in each culm, but sometimes there may be as many as three or four. These do not fit neatly into any one of the conventional categories of modified stems, but the term *corm* seems to be the least objectionable. The frequent reference to them as *bulbs* is acceptable only if this is taken to refer to their external appearance. They are not at all to be confused with the bulblets produced regularly in *Poa bulbos*a L. and occasionally in many other species where spikelets are modified into bulbs or small plants.

The occurrence of these corms is known in one or more species of *Arrhenatherum, Hordeum, Phleum, Alopecurus, Molinia, Phalaris, Panicum, Cinna, Holcus, Poa, Beckmannia, Colpodium, Ehrharta,* and *Melica,* and they are probably found in other genera. Their distribution in seven of the 15 recognized tribes is such that no phylogenetic significance can be attached to them (2). Neither is there any clear correlation between corm formation and ecologic conditions. The species which display it are well represented in the Mediterranean region and in the moist climates of Northern Europe, but some are found in other environments, and in any area the expression of the condition is erratic.

In such genera as *Phleum, Cinna,* and *Melica* there is usually only a single swollen internode, at about the ground level (Fig. 11), but in others such as *Arrhenatherum elatius,* var. *bulbosum* (Willd.) Spenner and *Panicum bulbosum* H.B.K., there may be as many as three or four, and the culms having them may grow in clusters of 15 or 20 or more (Fig. 10). Because of the peculiar appearance of such plants, some of them are popularly known as onion grasses. One report (3, 4) indicates that the variety of *Arrhenatherum* may even produce rhizomes whose swollen internodes give them the appearance of short strings of beads.

The internal anatomy of the corm is much like that of a rhizome. The corm is solid although the culm internodes above it may be hollow. In cross section it shows a cortical region surrounding a circle of vascular bundles set in a ring of sclerenchyma. The central parenchyma often contains vascular bundles, and its cells remain alive and display much seasonal physiological activity, indicating that food storage is involved (1). In some genera the predominant food is ordinary starch; in others, such carbohydrates as phlein, graminin, triticin, or inulin may be found. In a species of *Molinia* the parenchyma cells in the corm develop thick walls in autumn, and the following spring these walls dissolve and are probably used for food (1). This suggests that the reserve food is a hemicellulose.

The last stem anomaly to be mentioned is included more as a curiosity than as a thing of any particular morphological importance. It occurs in *Hymenachne*, a genus of aquatic grasses with about eight species in the tropics of both hemispheres. *H. amplexicaulis* (Rudge) Nees, of the American tropics, and the very similar *H. pseudointerrupta* C. Muell., of Southeast Asia, have been examined in some detail.

A cross section of the spongy submersed stem (Fig. 13) shows a thin layer of sclerenchyma next to the epidermis and then two rings of parenchyma separated by a ring of fibers. The vascular bundles are arranged in circles in the inner of these layers of parenchyma. All these tissues make up a shell around a central cylinder of parenchyma, which is devoid of vascular bundles. This core of parenchyma is the object of unique interest.

When the parenchyma cells are young, they are closely fitted together, with very small intercellular spaces. But as they mature during elongation of the internode, they are pulled apart until they assume the stellate form characteristic of the tissue of many other submerged aquatics (5) and (Figs. 13-15). These stellate cells form a series of transverse plates with enough longitudinal connections between the plates to hold the entire mass together so that the core of parenchyma can be punched out of the internode as an intact cylindrical mass. These long, terete cores are pliable and firm enough to be bent into various shapes. They can also be colored with various dyes. In the markets of Bangkok, and probably other cities of Southeast Asia, there can frequently be found on sale various ornamental objects in the form of flowers, birds, or animals made from these cylinders of pith (Fig. 12).

The late Dr. Agnes Chase, of the Smithsonian Institution, once told me that, in the hinterlands of Brazil, she had seen stems of *Hymenachne* used for wicks in crude oil lamps. A simple experiment with pieces of stems of the Asian species shows that they could be put to the same use. The unique structure of the central parenchyma provides an excellent capillary pathway for movement of the oil between the stellate cells. At present we know of no grass species outside the genus *Hymenachne* whose stems could be used in this way.

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