

Evolutionary History of the Grasses¹

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While some scientists have been working to sequence and describe the human genome, with increasingly dramatic results, another set of scientists has been quietly providing a map of evolutionary history, a time line that shows how life has evolved. Unlike the genome projects, which accumulate megabases of sequence from many genes in one organism, evolutionary projects accumulate megabases of sequence from the same handful of genes in many organisms. The scientists who investigate the pattern of evolutionary change are predominantly systematists, meaning, literally, those who study natural systems. Their work has three major goals. The first is to decipher the evolutionary history, or phylogeny, commonly drawn as a cladogram or branching diagram. Once that is accomplished, the second goal is to determine for each speciation event what sorts of changes must have occurred. The phylogeny allows us to define, for any point in time, what characteristics were ancestral (analogous to "wild type") and which were derived (analogous to "mutant"). If two species have a particular characteristic, such as white flowers or hairy leaves, then their ancestor is assumed to have had the same characteristic. If two species had different characteristics, then we look to their next closest relative to help determine the ancestral condition. This sort of deduction is based on assumptions about the likelihood of change and provides a hypothesis of evolutionary pattern, which can in some cases then be tested experimentally. The third goal of systematics is to create a formal classification that reflects history. There are many ways to convert an evolutionary tree into a hierarchical classification. The only hard and fast rule is that any named group should include all the descendants of a particular ancestor, i.e. should be a monophyletic group. This distinction between determining history and producing a classification is relatively recent. Until the last part of the 20th century, classifications were assumed to represent history, and the two investigations were conflated (Stevens, 1994).

To determine the evolutionary history of a group of organisms, systematists have traditionally used morphological characteristics, which are often difficult to study and require extensive developmental and anatomical investigation to establish appropriate comparisons. Because of the difficulties inherent in

studying form, many systematists now use DNA sequences to determine relationships among organisms. If large enough stretches of DNA can be compared for enough organisms, the phylogenetic relationships generally become clear. The need for large numbers of DNA sequences has led to collaborative groups of scientists who combine their data to reach a common goal. This is an unusual endeavor for systematists who traditionally have worked alone, each investigating a single group of organisms.

EVOLUTIONARY TREE OF THE GRASS FAMILY (POACEAE OR GRAMINEAE)

The grass family is of particular interest to humans. Most people on earth rely on grasses, including rice, wheat, and maize, for a major portion of their diet. Domestic animals are raised on diets partly or wholly of grasses. In addition, grasses form an important part of the urban and suburban landscape in much of the world. Members of the family also are ecological dominants, covering approximately 20% of the earth's land surface (Shantz, 1954).

The grass family includes approximately 10,000 species classified into 600 to 700 genera (Clayton and Renvoize, 1986; Watson and Dallwitz, 1999). The grasses are included with lilies, orchids, pineapples, and palms in the group known as the monocotyledons, which includes all flowering plants with a single seed leaf.

In the last couple of years, a clear picture has formed of the evolutionary history of the grass family. This comes from restriction site maps of the chloroplast genome (Soreng and Davis, 1998), sequences of chloroplast genes, including *ndhF* (Clark et al., 1995), *rpoC2* (Barker et al., 1999), *rbcL* (Barker et al., 1995), *matK* (Hilu et al., 1999), *rps4* (Nadot et al., 1994), and sequences of several nuclear genes, including phytochrome B (Mathews et al., 2000), GBSSI (Mason-Gamer et al., 1998), ITS (Hsiao et al., 1999), and 18S rDNA (Hamby and Zimmer, 1988). Although some of these studies have been hampered by small sample sizes or insufficient numbers of variable bases, all have reached similar conclusions about the order of events in the evolution of the grasses. The data from seven of these sources have been combined by a consortium of 13 researchers, who have called themselves the Grass Phylogeny Working Group (GPWG; www.virtualherbarium.org/GPWG/), and have produced a phylogeny (summarized in Fig. 1; see also Fig. 2; GPWG, 2000). This picture of the evolutionary his-

¹ This work was supported in part by the National Science Foundation (grant no. DEB-9815392).

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tory is strongly supported by bootstrap and decay analyses, statistics that measure the extent to which the data support the tree topology.

The GPWG chose 59 representative species for study of the phylogeny. These were chosen to represent all known major groups, plus a set of species whose relationships were unknown. We took advantage of earlier investigations that had studied sets of morphological characters across hundreds of species. For example, the Russian cytogeneticist Avdulov

(1931) reported on chromosome number and karyotype of many hundreds of grasses and found that a large group of temperate grasses had much larger chromosomes than other grasses, and fewer of them, with a base number of $x = 7$. This group includes such familiar species as wheat (*Triticum*), barley (*Hordeum*), rye (*Secale*), and oats (*Avena*), as well as most north temperate lawn and pasture grasses. The French anatomist Prat (1932) looked at the shape and structure of epidermal cells and found that the sub-

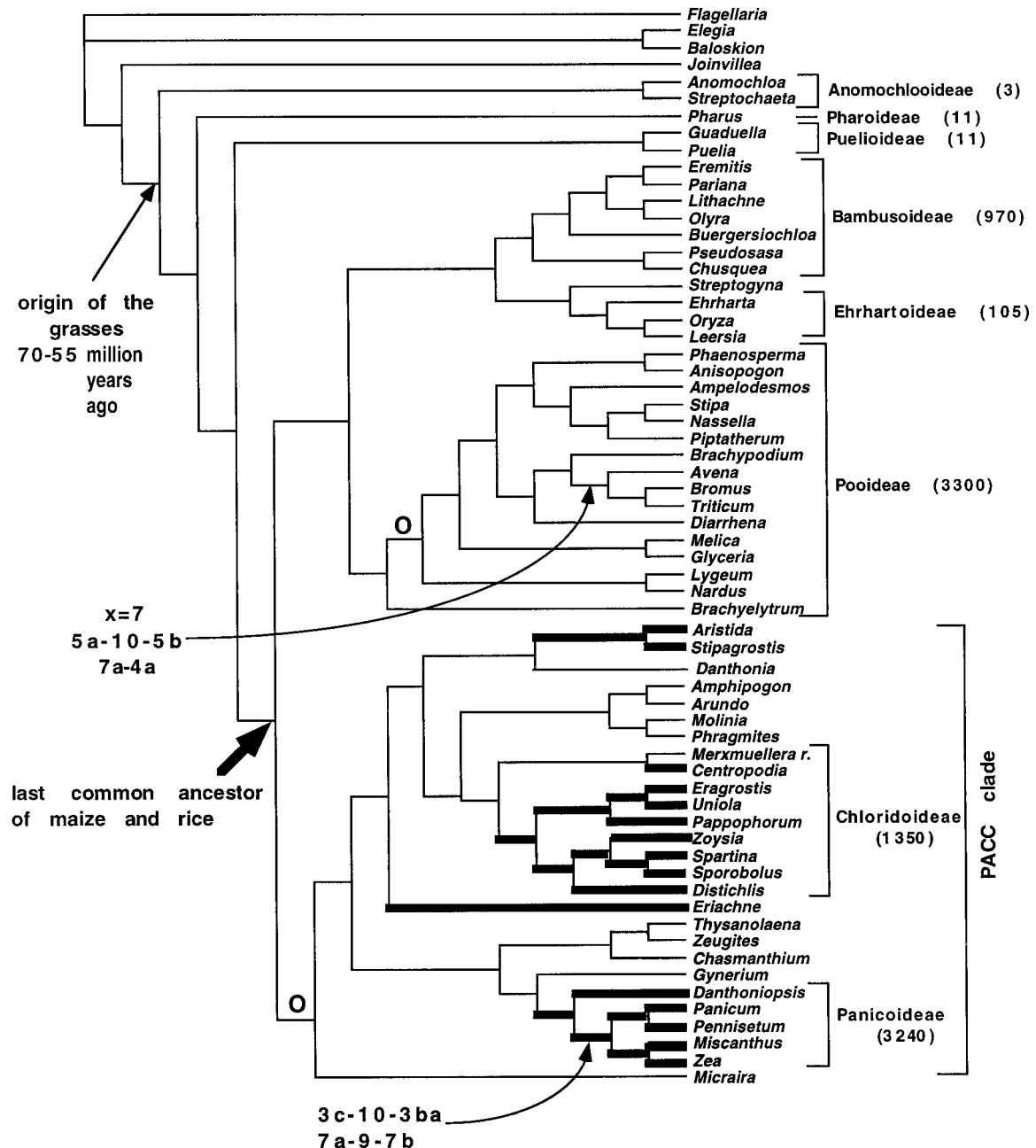


Figure 1. Phylogeny of the grass family based on combined data from chloroplast restriction sites, *rbcl*, *ndhF*, *rpoC2*, phytochrome B, ITS, GBSSI, and morphology (GPWG, 2000). Heavy lines indicate C_4 photosynthesis; numbers with hyphens indicate chromosomes formed from joining the appropriate rice chromosomes; O indicates shift to open habitats. Numbers in parentheses indicate approximate numbers of species.

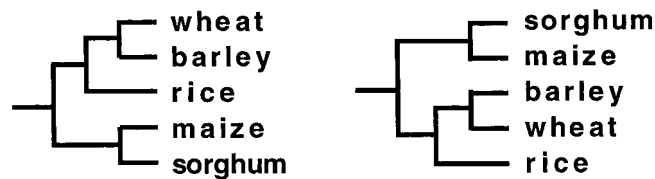


Figure 2. Reading phylogenetic trees. Phylogenetic trees are designed to show the relative order of speciation events. Species that are connected by a single branch point (node) are sister taxa. The more nodes separating two species, the more distantly related they are. The vertical arrangement of the names on the page does not reflect relationship and is chosen generally for convenience only. Thus, the two trees shown above represent the same evolutionary history, simply drawn differently.

sidiary cells of the stomata in Avdulov's $x = 7$ group have outer walls that are parallel rather than curved. This group, defined by cytological and anatomical characteristics, has also been found to represent a single lineage in every DNA study to date (for summary, see Kellogg, 1998; GPWG, 2000). The GPWG therefore decided to represent it by only three genera, *Avena*, *Bromus*, and *Triticum*, but it includes also barley, rye, and all the cool season grasses commonly placed in subfamily Pooideae.

The phylogeny correlates well with information from mapping of the nuclear genome (Kellogg, 1998). In the nuclear genome, genes are in a similar order in all grasses (Gale and Devos, 1998). Thus whole chromosomes of rice can be lined up with chromosomes of wheat or maize. Major re-arrangements have occurred, however, among blocks of linked genes, and these correlate with the phylogeny. For example, in the panicoid grasses maize (*Zea*), sugar cane (*Saccharum*), sorghum (*Sorghum*), pearl millet (*Pennisetum*), and foxtail millet (*Setaria*), the linkage group corresponding to rice chromosome 10 is inserted into the middle of what had been rice chromosome 3. The centromere of 3 is apparently replaced by the centromere of 10, which is now the centromere for the entire combined chromosome. Rice chromosome 9, similarly, has been inserted in rice 7. Other rearrangements have occurred in the subfamily Pooideae (Fig. 1), correlating with the change in chromosome number to $x = 7$ and a marked increase in genome size (Bennetzen and Kellogg, 1997).

From the phylogeny, the GPWG has produced a revised classification, shown in part in Figure 1.

Names of plants are governed by the International Code of Botanical Nomenclature (<http://www.bgbm.fu-berlin.de/iapt/nomenclature/code/default.htm>), analogous to the standards developed for Arabidopsis or maize gene nomenclature (Meinke and Koornneef, 1997) at http://www.agron.missouri.edu/maize_nomenclature.html#1996UPDATES (Beavis et al., 1995). All species must be placed in a genus, so a species name consists of the familiar binomial. Genera are then assembled into families, and the families are assembled into orders. For convenience, a large

family may be divided into subfamilies, subfamilies into tribes, and tribes into subtribes. All these intermediate ranks are used in the grass family because it is so big. Subfamily names conventionally end in -oideae, tribes in -eae, and subtribes in -inae. Some taxonomists are suggesting that a ranked classification should be dropped as it may be cumbersome and confusing, but this proposal has not yet received wide support.

Previous classifications were created using only characters that could be observed on pressed dried specimens. Molecular data have shown that some groups so delimited were accurate in reflecting evolutionary history, but some changes have been necessary.

Each group with a name is required to represent only a single lineage. Given that criterion, we tried to make the named subfamilies as similar as possible to those that previous workers had recognized. Thus, for much of the family, the classification is similar to those presented by Watson and Dallwitz (1999) and Clayton and Renvoize (1986). The Pooideae includes Avdulov's $x = 7$ group but is expanded to include some genera whose relationships had only been guessed at by previous workers. The Panicoideae, including maize, sorghum, common millet, and foxtail millet, has been recognized since the time of Robert Brown (1810, 1814), and remains largely unchanged; its members all have paired flowers with the upper one generally hermaphrodite and the lower one staminate or reduced. The Chloridoideae, including finger millet and tef, was originally recognized by the structure of its microhairs and its C_4 anatomy. The Bambusoideae, including the woody and herbaceous bamboos, is characterized by asymmetrically lobed mesophyll cells (Zhang and Clark, 2000). In its new circumscription, it represents a much smaller group than it has in the past. Together these four subfamilies account for nearly 90% of the species in the grasses.

The major point of discussion has been the disposition of the large group including the panicoids and chloridoids, known by the acronym PACC (panicoids, arundinoids, chloridoids, and centothecoids) in much of the recent literature. Although the entire group could have been designated a single large subfamily, the only morphological characteristic they share is a long internode in the embryo below the leaves around the point of attachment of the presumed cotyledon (mesocotyl), a character difficult to observe under most ordinary circumstances. The revised classification thus recognizes Chloridoideae and Panicoideae, as indicated in Figure 1. The remaining groups are given names or are left incertae sedis, i.e. "of uncertain placement."

DINOSAURS DID NOT EAT GRASSES

The origin of the grasses can be dated by the appearance of grass pollen in the fossil record. The

grasses and their relatives have distinctive pollen that is nearly spherical and with a single pore. Grass pollen itself can be distinguished by minute channels or holes that penetrate the outer, but not the inner, pollen wall (Linder and Ferguson, 1985). The earliest firm records of grass pollen are from the Paleocene of South America and Africa, between 60 and 55 million years ago (Jacobs et al., 1999). This date is after the major extinction events that ended the age of dinosaurs and the Cretaceous period.

Additional fossil pollen grains that may be grasses or may be grass relatives have been found in Maastriichtian deposits of Africa and South America (approximately 70 million years ago); these were fossilized just before the end of the Cretaceous. Because of the way the pollen was preserved, however, it is impossible to tell whether it had the channels in the outer wall that are characteristic of the grasses (Linder, 1987; Jacobs et al., 1999).

These pollen grains give upper and lower bounds for the date of the ancestor of the grasses (arrow in Fig. 1). Based on the fossil record, this ancestor lived before 55 million years ago but probably after 70 million years ago. This range of dates is used to calibrate molecular clocks, which are then used to calculate the times of other events in the history of the grasses (Box 3).

WHAT HAPPENED WHEN THE GRASSES ORIGINATED

By comparing grasses with their closest relatives (outgroups), we can infer what sorts of changes must have happened at the node with the arrow, right around the end of the Cretaceous or the beginning of the Tertiary period. A major change occurred in the timing of embryo development. Most monocotyledonous plants have largely undifferentiated embryos. Seed maturation begins after the embryo has formed a shoot apical meristem, but the differentiation of cotyledon, leaves, root meristem, and vasculature largely occurs after the seed is shed from the parent plant. In the grasses, embryo development is accelerated relative to seed maturation (Kellogg, 2000).

At the same time there was a notable change in the structure of the fruit. All the ancestors of the grasses had ovaries formed of three fused carpels, each carpel forming one locule with one ovule (Kellogg and Linder, 1995). In many of the close relatives, and we presume in the grass ancestors, two of those ovules abort and only one develops (Dahlgren et al., 1985; Linder, 1991). In the grasses, only one locule and one ovule ever form. As the ovule develops the outer integument fuses with the inner ovary wall to form the distinctive fruit of the grasses, known as the grain or caryopsis. This structure is unique among the flowering plants.

THE GRASS SPIKELET ORIGINATED IN SEVERAL STEPS

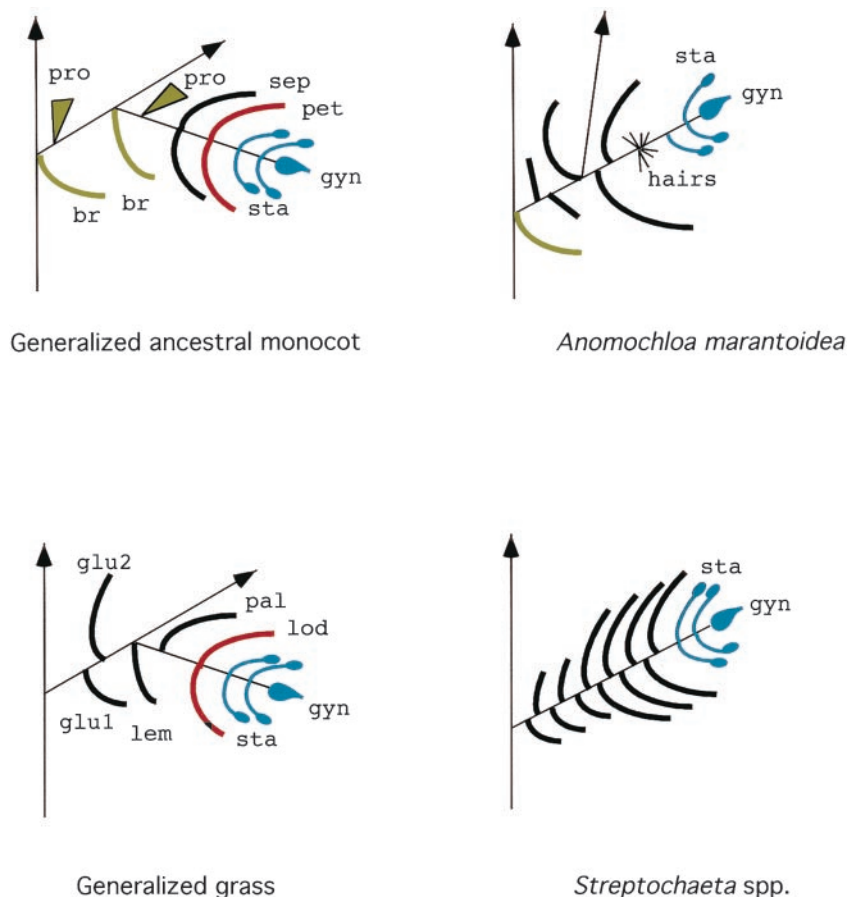
The most striking characteristic of grasses today is their floral and inflorescence structure. Grass flowers are generally arranged in little spikes, or spikelets; each spikelet consists of one or more flowers plus associated bracts (Fig. 3). In most species, the gynoecium has two stigmas and the androecium has three stamens. Outside the stamens, in the position of petals, are generally two flap-like structures, the lodicules, that become turgid and force the flower open at anthesis. Outside the lodicules is a structure similar to a prophyll, a two-keeled, leaf-like structure that normally appears on an axillary branch. The prophyll-like structure is the palea, and outside that is a bract-like structure (the lemma). Together these make up the floret. Florets are borne singly or in groups and are subtended by two more bracts (the glumes).

The phylogeny shows that the spikelet must have originated in several steps (GPWG, 2000). The earliest grasses had three stigmas, a relict of the three fused carpels that they inherited from their ancestors; this number was reduced to two after the speciation event that led to *Pharus*. The earliest species also had, like their non-grass ancestors, six stamens. It is not clear from the phylogeny precisely when the shift from six to three occurred, but it must have been after the divergence of the *Guaduaella/Puelia* group.

The ancestry and origin of the lodicules, palea, lemma, and glumes have been the subject of a vast and largely inconclusive literature. Recent work on lodicules in maize and rice has shown that they express petal-identity genes (Ambrose et al., 2000; Kyozuka et al., 2000). Because they are in the position of petals and because the early grasses have three, rather than just two, it seems likely that lodicules represent modifications of petals. However, the third lodicule when present is inserted higher on the floral axis than the other two, which has suggested to some authors that it has a different evolutionary origin (for review, see Clifford, 1987). It is curious that neither *Anomochloa* nor *Streptochaeta*, the earliest lineage of the grasses, has either petals or lodicules, although *Anomochloa* has a ring of hairs outside the stamens (Fig. 3). This means that either lodicules originated in the first grasses and were lost in *Anomochloa* and *Streptochaeta* or that they evolved after the grass family originated.

If lodicules are modifications of petals, could the palea and lemma be modifications of sepals? This has been suggested but will have to await additional genetic data. *Anomochloa* and *Streptochaeta* do not have structures that can be confidently called either lemmas or paleas. It thus seems likely that the conventional grass spikelet originated after the first grasses and characterizes most but not all of the family.

Figure 3. Diagram of a generalized monocot inflorescence, inflorescences of *Anomochloa marantoidea* and *Streptochaeta* spp., and a generalized grass spikelet. Bracts and prophylls are in green, androecia and gynoecia in blue, and petals and lodicules in red. *Anomochloa* has only four stamens and is thus shown with an incomplete outer whorl. Structures in black have uncertain homologies. br, Bract; pro, prophyll; sep, sepal; pet, petal; sta, stamens; gyn, gynoecium; glu1, first glume; glu2, second glume; lem, lemma; pal, palea; lod, lodicule.



WHAT HAPPENED BEFORE THE GRASSES ORIGINATED

Some characters associated with the success of the grass family evolved long before the first grass appeared in the forest and thus cannot be used to explain their current ecological dominance. The grasses are wind-pollinated but so are all their relatives (Linder and Kellogg, 1995). From this we can infer that wind-pollination originated millions of years before the grasses appeared on earth. Along with wind pollination comes a reduction in perianth size and loss of pollen stickiness (Linder, 1998). All the relatives of the grasses similarly accumulate silica somewhere in the plant so that silica accumulation also must have originated well before the grasses themselves did. In addition, a large set of monocotyledonous plants, including not only the grasses, but also the ginger, pineapples, and palms, have cell walls rich in ferulic acid. Ferulic acid in the cell walls must therefore be an ancient characteristic preserved in the grasses.

WHAT HAPPENED AFTER THE GRASSES ORIGINATED

Other "grass" characteristics originated long after the first grasses (GPWG, 2000; Kellogg, 2000). The

most notable of these is drought tolerance and the capacity to grow and thrive in dry open habitats. The original grasses were plants of forest margins or deep shade, characteristics that are retained today in *Anomochloa*, *Streptochaeta*, *Pharus*, *Puelia*, *Guaduella*, the bamboos, and the basal pooid, *Brachyelytrum*. The phylogeny shows that the grasses persisted for many millions of years, and apparently did not diversify much in such habitats. The shift in habitat occurred at the points marked by O on Figure 1. This preceded the major diversification of the family, detected in the fossil record by a marked increase in the amount of grass pollen in the mid-Miocene epoch (Jacobs et al., 1999).

MULTIPLE STARTING POINTS, SAME DESTINATION

The evolutionary tree can be used to determine major evolutionary changes. One that has been especially well studied is C_4 photosynthesis, which is a complex addition to the conventional C_3 photosynthetic pathway (Kanai and Edwards, 1999; Fig. 4). In all C_4 species, the C_3 pathway is sequestered in the bundle sheath cells that surround the vascular tissue; this is done in part by suppressing expression of ribulose 1,5 biphosphate carboxylase/oxygenase

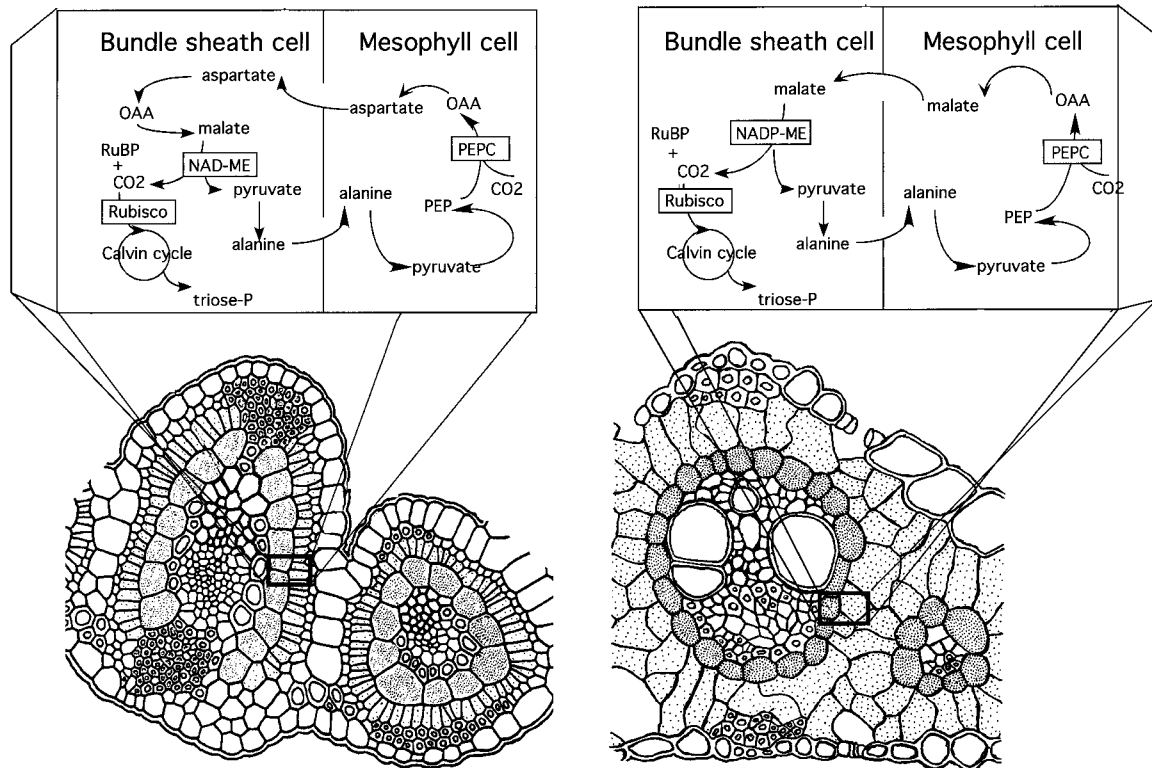


Figure 4. Comparison of anatomy and biochemistry of two major C₄ photosynthetic types. On the left is *Bouteloua breviseta* (redrawn from Esau, 1977), an NAD-ME species with two bundle sheaths, the outer of which fixes carbon. On the right is *Echinochloa crusgalli* (redrawn from Gould and Shaw, 1983), an NADP-ME species with a single bundle sheath. Enzymes are boxed. NAD-ME, NAD-malic enzyme; NADP-ME, NADP-malic enzyme; PEPC, phosphoenolpyruvate carboxylase; RuBP, ribulose 1,5-bisphosphate; triose-P, triose phosphate.

(Rubisco) in the mesophyll. Phosphoenol pyruvate carboxylase is then used to attach bicarbonate to phosphoenolpyruvate (PEP), creating a four-carbon compound, oxaloacetate (OAA).

C₄ grasses are the most common species in the prairies of North America, the vast grasslands of Africa, and the llanos and cerrados of South America. Studies of ancient ecosystems have shown that these broad areas developed 5 to 6 million years ago. The earliest record of C₄ photosynthesis is based on isotopic ratios and is dated at 15 million years ago (Kingston et al., 1994; Latorre et al., 1997), and the earliest leaf fragment that can be confidently designated C₄ is dated at 12.5 million years ago (Nambudiri et al., 1978).

A molecular clock estimate, however, places the origin of the predominantly C₄ subfamily Panicoideae much earlier at 25 to 32 million years ago (Gaut and Doebley, 1997).

It is common to use numbers of mutations between two species to estimate the time since they diverged. Statistical tests will determine whether the rate of mutation is approximately constant over time. The clock then must be calibrated with a fossil or a well-documented geological event; this provides an estimate of number of mutations per year. Given this calibration, the divergence of other species can then

be estimated. The discrepancy between the fossils and the molecular clock could indicate that the clock was mis-calibrated or alternatively that C₄ grasses were originally quite rare and thus are hard to find as fossils. The latter explanation suggests that C₄ grasses persisted as minor components of the flora for many years before they became ecologically dominant (Kellogg, 1999).

Placing C₄ photosynthesis on the evolutionary tree shows that it originated multiple times among several closely related subfamilies (Fig. 1; Kellogg, 1999, 2000). Extensive studies of anatomy, histology, biochemistry, and gene expression have shown that the C₄ pathway did not evolve the same way each time it originated (Sinha and Kellogg, 1996).

Most studies of the biochemistry of C₄ photosynthesis have proceeded on maize. Like most other C₄ panicoids, maize has only one layer of cells surrounding its vascular bundles; this represents a loss of one layer of bundle sheath cells. In maize the OAA produced in the mesophyll is reduced to malate, which is moved into the bundle sheath, and one carbon is removed by NADP-malic enzyme. That carbon is picked up by Rubisco, and the remaining three-carbon compound is moved back to the mesophyll where it is phosphorylated to regenerate PEP.

In the Chloridoideae, on the other hand, all species are C_4 but have two layers of cells around the vascular bundles, a characteristic that they share with all their C_3 ancestors. In these the OAA is aminated, rather than reduced, and Asp is moved into the bundle sheath, where the fourth carbon is removed by NAD-malic enzyme. Phosphorylation of the three-carbon compound apparently occurs in the bundle sheath rather than in the mesophyll (Sinha and Kellogg, 1996).

The evolutionary tree thus shows that C_4 has originated multiple times. This then led to more detailed investigations, which showed that gene-level changes apparently have happened differently each time.

CONCLUSIONS

The collaborative work of the GPWG has resolved the broad outline of grass phylogeny, and we now know with considerable confidence which species are most closely related. This has produced a number of surprises, including the gradual evolution of the spikelet, the relatively late shift into open habitats, and the apparently recent diversification of the family. Additional systematic studies are continuing to place more and more grass species on phylogenetic trees providing an increasingly precise view of the order of evolutionary events.

This lays the groundwork for the main enterprise of evolutionary biology, that of understanding precisely what sorts of changes have occurred at critical junctures in evolutionary time, and therefore how evolution must have worked. For example, the close relationship of the chloridoid and panicoid grasses, along with other C_4 species, suggests the possibility of underlying physiological similarities. Defining the derived states in terms of specific mutations will require new molecular tools, possibly of the sort now being developed for functional genomics. As such work proceeds, we will be able to define more and more precisely the genetic background that characterizes particular groups of grasses.

The phylogeny shows nested sets of species increasingly distantly related to the cereal crops. These certainly contain novel alleles or combinations of alleles that affect agronomically important phenotypes. The challenge of the future is to use the crop species as windows on the spectacular diversity produced by evolution and at the same time to use the thousands of wild grasses as tools to help understand the cereals.

ACKNOWLEDGMENTS

Thanks to J. Barber, M. Beilstein, A. Doust, H. Davis, B. Gunn, S. Malcomber, S. Razafimandimbison, and P. Sweeney for helpful comments on the manuscript and for

suggesting I take out the bit about the cat. Also, thanks to editor A. Hirsch and two anonymous reviewers for their comments.

Received November 7, 2000; accepted December 19, 2000.

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