

South With the Spring: A Story of Evolution and Tree Buds

Stanley Rice

Southeastern Oklahoma State University

I write from Bryan County, Oklahoma, named after you-know-whom: William Jennings Bryan. After a lifetime of fighting for the causes of the common man, what is he remembered for? His final and fatal attempt to block the teaching of evolution in Tennessee at the Scopes Trial. He won and lost. Actually, it was not so much the science of evolution as the abuses of social Darwinism, with its celebration of strong people vanquishing the weak, that bothered this great statesman. And today, among the people of Bryan County, Oklahoma, it is not so much the science of evolution as the anti-religious sentiments that they imagine to accompany it that bothers this Christian, and conservative, population. And here I am, a biology professor who teaches evolution. What do I do? Do I try to be nice, or do I dangle evolution right in their faces?

Stanley Rice received his PhD in plant biology from the University of Illinois at Urbana-Champaign in 1987. He taught botany and other biology courses in New York, Indiana, and Minnesota, before joining the faculty of Southeastern Oklahoma State University in 1998.

I do both. I dress up like Charles Darwin (which, with my gray beard, requires only a Victorian hat and a ribbon tie) every February 12 (Darwin's birthday) and every October 12 (Discovery Day, also known as Columbus Day) for my spring and fall semester classes. I leave them with no doubt about the DNA and fossil evidence for human evolution — the part they find most threatening. But I also tell them about the differences between science and religion, and develop at some length a defense of their mutual compatibility. I tell them of my own Christian faith and how it is deepened by an understanding of evolutionary science — yes, even while I am standing there in my Darwin suit.

And I also tell them a story about tree buds and evolution. A fundamentalist who may get upset over ape-men is unlikely to become angry over tree buds. And while Lucy's bones and those of the Nariokotome boy hide in distant museums, my fellow Oklahomans cannot avoid an encounter, every spring, with the bursting of the buds of deciduous trees and shrubs. As a botanist, I want not only to teach evolution, but also to get my students just to *notice* the great spectacle of

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AUTHOR'S ADDRESS

Marshall D Sundberg
Department of Biological Sciences
Emporia State University
Emporia KS 66801
sundberm@esumail.emporia.edu

botanical springtime, at which they might never have looked closely.

As spring temperatures move north, life awakens: a beautiful spectacle recorded by Edwin Way Teale in his classic *North With The Spring* (Teale 1951). In any one location, the tree buds seem to burst all at once, very quickly. The rapid burst of buds occurs because the tissues of the leaves and flowers formed in the buds the previous autumn and were quietly waiting for springtime. When spring arrives, the tissues need only swell with water and burst away the scales.

But although the buds burst quickly, they do not burst all at once. Some trees and shrubs open their buds earlier than others. When I lived in Minnesota, I noticed that almost all the buds burst within a period of 2-3 weeks. But down here in Oklahoma, spring is much longer — a full two months elapses between the emergence of the American elm in February and that of the pecan in April.

In the spring of 2000, my plant taxonomy students and I did more than just notice this pattern; we also documented and analyzed it. The plant taxonomy class in 2002 repeated the project with very similar results. At the very least, having students keep records of which trees open their buds on which dates can get them to notice the tremendous diversity of tree and shrub species — we had 40 species in our study in spring 2000. But this activity can also contribute to worldwide research. Students all over the world record tree budburst dates and send them to the GLOBE program (<http://www.globe.gov>), where these data will be analyzed to detect the extent that global warming may be causing spring to come earlier in temperate climates (NOAA 2001). But we wanted to go further. We wanted to know *why* some tree species opened their buds earlier than others.

There are several possible reasons for the differences in budburst time. "Proximate" factors include patterns of temperature and changes in day length. Buds of deciduous trees may open earlier in a warm than a chilly springtime; however, a warm winter may have the surprising effect of *delaying* budburst because the winter warmth prevented breakdown of chemicals that inhibit budburst (Murray and others 1989). But we were interested primarily in "ultimate" factors — *evolutionary* ones.

The first flowering plants apparently evolved just before the early Cretaceous period, about 120 million years ago. At this time, the great world-continent of Pangaea had broken up; the Tethys seaway was separating the southern, equatorial continent (formerly Gondwanaland, later to become South America, Africa, Australia, India, and Antarctica) from the northern, temperate continents (remnants of Laurasia, later to become North America, Greenland, and Eurasia). Great forests emerged in the north temperate regions, with some deciduous trees, and some warm-evergreen trees. While the flowering plants as a group have a tropical origin, not all flowering plant families do. Some of the trees in the north temperate forests were in families that had evolved in the north temperate region, and others were in families that had migrated from the tropical south. During early Tertiary times, before about 30 million years ago, the climate

was warm and even, and deciduous forests grew up to very high latitudes. By this time, all of the families of flowering plants had evolved (Jones and Luchsinger 1986: 118).

In the second half of the Tertiary, cycles of cooling began (see Wolfe 1987 for more information), culminating in the Ice Ages of the past 2 million years. The populations of trees either had to die, which many did, or adapt. They could adapt in either of two ways. They could *avoid* the cold — by restricting their range to regions in which frost damage was less likely — or they could *tolerate* the cold.

Cold temperatures damage plant tissues primarily by causing ice to form within them. While the ice crystals may puncture cell membranes, it turns out that the main problem is freeze-drying (Pearce 2001). The ice forms outside the cells, causing the insides of the cells to desiccate. In order to tolerate this, the plant's cells must have chemicals that help them to adjust to the dry conditions. Buds generally have these adaptations, but once a bud opens, the tissues may or may not have this protection. Plant families that have existed for a longer period of time in regions that have cold winters contain more cold-tolerant species than plant families that have existed in these regions for a shorter period of time.

For those trees that protect their young leaves and flowers from frost, there is a price to pay: they must use their materials and energy to manufacture these protective molecules and to *tolerate* the cold temperatures of a spring frost. The benefit that they receive is that they can open their buds earlier in the spring, even though there remains a risk of frost. In so doing, they can take advantage of wind pollination, or they can begin to spread their leaves sooner. They may thereby be able to reproduce sooner than, and to shade out, the other, slower species. The (evolutionary) reason that trees even exist at all is not to get their leaves closer to the sun — which is, after all, 93 million miles away — but to get their leaves higher *than those of other plants*. Or, to outdo their competitors in another way, they may open their leaves sooner than those of other plants.

For those trees that do not protect their young leaves and flowers from frost, there is a price to pay. By waiting until all (reasonable) danger of frost is past (that is, by *avoiding* it), they may have to grow their leaves in the shade of the earlier plants. But at least they do not need to expend energy on the protective molecules.

Some tree species produce flowers before leaves, and others produce leaves before flowers. For this investigation, we assumed that there would be a disadvantage if the trees sustained frost damage to either flower or leaf buds, and therefore they would protect either type of bud by tolerating or by avoiding the low temperatures.

Both groups of plants — the tolerators and the avoiders — are adapted to the climatic conditions we have today in North America; it is just that they are adapted in different ways. The hypothesis that my students and I tested was *plants whose ancestors evolved in temperate latitudes are more likely to tolerate frost better; and to open their buds earlier; than plants whose ancestors evolved in tropical latitudes.*

METHODS

Gathering the data to test this idea was simple but tedious. We had to record the budburst dates of as many trees as we could find. Each pair of students had to find 20 trees, of as many species as they could locate, and monitor them daily or as close to daily as they could. In addition, I also monitored numerous trees. We used the GLOBE protocol for assigning budburst dates (NOAA 2001). We gathered data from two locations — Tulsa, Oklahoma, latitude 36°N; and in the vicinity of Durant, Oklahoma, and in nearby areas of north Texas, latitude 34°N. These data sets will be hereinafter referred to as northern Oklahoma and southern Oklahoma.

We did not monitor budburst in every individual or every species that we encountered. We used these rules to decide which trees to measure: First, we chose only species native to eastern Oklahoma. For example, we omitted the Bradford pear (*Pyrus calleryana*) and white mulberry (*Morus alba*). Second, we omitted species that are commonly propagated by horticulturalists, even if native. For example, redbuds (*Cercis canadensis*), flowering dogwood (*Cornus florida*), and pin oak (*Quercus palustris*) are native to eastern Oklahoma, but many of the individuals may have been planted from genetic sources outside of Oklahoma. Non-native species and genotypes may burst their buds in response to environmental conditions different from those that would induce budburst in native stock. Third, we avoided juvenile individuals. Fourth, for species that spread clonally such as poison ivy (*Toxicodendron radicans*), we chose ramets that were distant from one another and not likely to be in the same clade. Fifth, we avoided damaged individuals (for example, those with heavy mistletoe infestation). Aside from these restrictions, we monitored as many individuals of as many woody species as possible. This analysis used 513 trees from 40 species in 22 families. This sample obviously included a great deal of individual variation due both to local climate and to genetic diversity. We included this variation deliberately, in order to determine whether the hypothesis is correct despite local variations.

Then we analyzed the data. The level of statistical sophistication for analyzing the data can be adjusted to suit the class; in a high school class, for example, you may be content with a simple graph of the results (as in Figure 1). We used a computer-based analysis of variance. The independent variables in the main analysis were: (1) family origin (temperate versus tropical); and (2) species, nested within families. We conducted separate analyses to examine other hypotheses (see Discussion), in which we included, along with family origin, (3) pollination mode (wind versus animal), (4) wood type (diffuse- versus ring-porous). Our analyses also explored how variables may have interacted in complex ways. The response variable was budburst date (using February 1 as Day 1). We analyzed northern and southern Oklahoma trees separately. Each individual tree was an observation in this analysis. We used an analysis in which the statistical significance of the relationship of independent variable with the response variable was tested after the others had

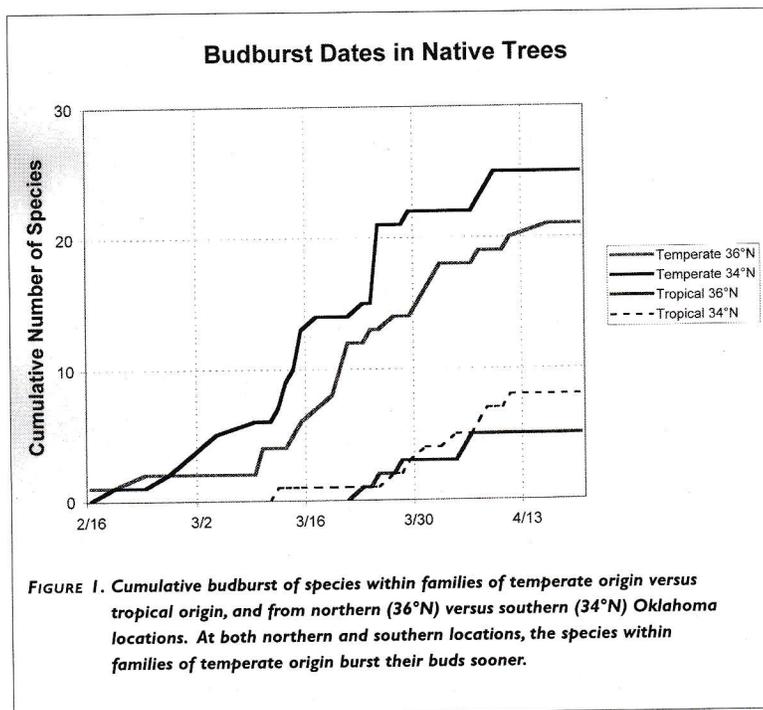


FIGURE 1. Cumulative budburst of species within families of temperate origin versus tropical origin, and from northern (36°N) versus southern (34°N) Oklahoma locations. At both northern and southern locations, the species within families of temperate origin burst their buds sooner.

already been included. In this article, I focus primarily on the results of temperate versus tropical origin of the family, which tests the main hypothesis stated in the introduction.

There are two ways to determine whether a plant family is of temperate or tropical origin. First, the part of the world with the most species within the family is likely to be where the family evolved. We consulted the plant family distribution maps in Heywood (1978) to collect information on the worldwide distribution of living plant species within families. Second, fossil evidence indicates the part of the world and the time of origin. We used the information contained in Raven and Axelrod (1974) for this determination. The two sources of information coincided closely and gave the same results in the analysis below. Of course, this simplistic classification of plant families as temperate or tropical incorporates a great deal of variation; some tropical families, for example, may have originated in tropical highlands under climatic conditions more similar to those of north temperate regions. However, in order to use this exercise as an investigation for students or a demonstration for lay people, we cannot include the full complexity of factors that are involved in the study of historical plant geography. As just one example, the elm family, Ulmaceae, consists of two subfamilies, the primarily temperate Ulmeae and the primarily tropical Celtidae; however, for this analysis, we consistently used family, not subfamily, as the basis of classification, so elms were considered temperate.

RESULTS

In both northern and southern Oklahoma, woody plants in families of temperate origin opened their buds earlier than woody plants in families of tropical origin: an average of 12 days earlier in southern

Oklahoma, and 5 days earlier in northern Oklahoma. This pattern is clearly visible in Table 1, which lists average budburst dates of species in temperate families and species in tropical families in separate columns. Figure 1 also shows that species in families of temperate origin open their buds earlier than species in families of tropical origin. Table 1 and Figure 1 separate the northern and southern Oklahoma data sets, both of which show the pattern. The analysis of variance showed a significant difference between families of tropical and temperate origin, and significant differences among the species within the tropical and temperate categories, both at the $p < 0.0001$ level, for both northern and southern Oklahoma data sets. This indicates that there is less than 1 chance in 10 000 that the results are not explained by the hypothesized relationship.

This analysis was conducted on individual trees. This is a valid procedure, since each individual tree has its own budburst date. The variation of budburst dates within each tree species has been noticed at least since Darwin wrote *The Variation of Plants and Animals Under Domestication*. However, the same pattern emerges when we analyze the *average* budburst times of each *species*. In order to obtain a sufficiently large sample size for an analysis that used only the means, I had to merge the northern and southern Oklahoma data sets into a two-way interactive analysis of variance, which can determine the significance of two different factors in one data set. In this analysis, the only factor that was significant (at a probability level of $p = 0.029$) was temperate-versus-tropical evolutionary origin. Therefore, we reach the same conclusion whether we analyze the trees or analyze the species.

DISCUSSION

It is important to reiterate that the species of woody plants we studied are all, *today*, temperate species; the temperate-versus-tropical origin represents a *vestigial* effect of evolution — trace characteristics that point to the organism's evolutionary past. For many "perfect" adaptations of the present, a creationist could say that the Creator made it that way; but for leftover processes from the past, such an argument is not credible (Gould 1980). To counter the anti-evolutionists' argument that we see evolution in all data sets because that is what we *want* to see, it is important to point out that we detected other patterns of variation in these data than the evolutionary one we were studying.

One of these patterns involves the *anatomy* of the trees. Each year, the trunk of a tree adds a new layer of wood. The wood consists largely of xylem, the cells that transport water from the roots through the trunks up to the leaves. Some of the cells of the xylem are large — some large enough to see with the unaided eye — while most are small. In some species, the *ring-porous* species, many large vessels are produced in the spring, and few or none during the summer; the large vessels therefore form a ring in just the spring wood. Other species are *diffuse-porous* because their large vessels, if any, are scattered through all of the wood layer. Large vessels are great at transporting water. In fact, a large vessel that is 3 times as wide as

a small vessel can theoretically transport *81 times* as much water as the small vessel. The problem is that most of the large vessels are damaged, usually *permanently*, during the winter. A tree with *diffuse-porous* wood, in the spring, can rely on last year's wood — or even the wood from several previous years — to transport its water up so that it can burst the buds. But a tree with *ring-porous* wood has lost the use of most of its wood from last year, and of course from previous years — even though that wood is still there, helping to hold the tree up, it does not help much in the transport of water up to the buds. Trees with *ring-porous* wood, therefore, must start growing a new layer of wood before they can burst their buds. For this reason, it has been noted (for example, by Lechowicz 1984) that trees with *diffuse-porous* wood can get an earlier start in the spring. One of our analyses indicated that *diffuse-porous* species burst their buds sooner than *ring-porous* species (data not presented). However, even after the effects of wood type are included in the analysis, the temperate-versus-tropical distinction is still statistically significant. There are many exceptions — the earliest-budding species of tree in our study, the *ring-porous* American elm, being one (see Table 1 for the wood types in the species we studied).

Another pattern involves the *ecological interactions* of the trees. The earliest buds to burst are the flowers of the wind-pollinated trees such as elms and cottonwoods. Wind-pollinated flowers are small, and usually lack petals and nectar. Petals provide no advantage in attracting wind-borne pollen; in fact, they just get in the way of the wind's picking up pollen from some flowers and depositing it in others. These tiny, numerous flowers usually open before the leaves emerge, for the leaves, too, would interfere with the movement of pollen. Finally, the winds are, on the average, stronger in the early spring than in the late spring and summer. Insect-pollinated flowers (and those like trumpet creeper that are pollinated by hummingbirds) open later, when the insects and birds become active. This same pattern appears to occur in these data sets; however, upon analysis, these patterns turn out not to be significant, perhaps because there are many exceptions. While there are no insect-pollinated flowers that open in the very early spring, the insect-pollinated black cherries and wild plums open well before the midpoint of spring; and some wind-pollinated trees such as pecans open both flower and leaf buds as late as mid-April (see Table 1 for the types of pollination used by the species we studied).

Although these anatomical and ecological factors influenced budburst time, the statistically most significant factor was temperate-versus-tropical evolutionary origin. We also infer that the pattern based on evolutionary origin must have preceded the others. For example, it was only the trees whose ancestors evolved in temperate regions that were able to take advantage of the early spring winds for wind pollination. Only the trees that could tolerate spring frosts — and whose ancestors came from the temperate zone — could open their wind-pollinated flowers in February and early March.

Some of the species were more abundant than others. However, this is unlikely to have influenced the

TABLE I.

AVERAGE BUDBURST DATES OF WOODY SPECIES IN OKLAHOMA

Family: species	Common name	TEMPERATE FAMILIES		TROPICAL FAMILIES	
		Date northern Oklahoma	Date southern Oklahoma	Date northern Oklahoma	Date southern Oklahoma
Ulmaceae: <i>Ulmus americana</i> ^b	American elm	19 Feb (5)	16 Feb (11)		
Ulmaceae: <i>Ulmus alata</i> ^b	Winged elm		23 Feb (15)		
Aceraceae: <i>Acer saccharinum</i>	Silver maple	26 Feb (11)	28 Feb (6)		
Hamamelidaceae: <i>Liquidambar styraciflua</i>	Sweetgum		2 Mar (12)		
Rosaceae: <i>Prunus angustifolia</i> ^a	Wild plum		4 Mar (3)		
Aceraceae: <i>Acer negundo</i>	Boxelder	11 Mar (6)			
Vitaceae: <i>Vitis rotundifolia</i> ^a	Wild grape	11 Mar (4)			
Fagaceae: <i>Quercus velutina</i> ^b	Black oak	15 Mar (15)	10 Mar (4)		
Oleaceae: <i>Fraxinus pennsylvanica</i> ^b	Green ash	21 Mar (6)	9 Mar (3)		
Lauraceae: <i>Sassafras albidum</i> ^a	Sassafras				12 Mar (4)
Salicaceae: <i>Populus deltoides</i>	Cottonwood	19 Mar (18)	13 Mar (5)		
Aceraceae: <i>Acer saccharum</i>	Sugar maple		14 Mar (3)		
Rutaceae: <i>Zanthoxylum clava herculis</i> ^a	Hercules' club		14 Mar (2)		
Rosaceae: <i>Prunus serotina</i> ^a	Black cherry		15 Mar (2)		
Fagaceae: <i>Quercus marilandica</i> ^b	Blackjack oak		17 Mar (8)		
Platanaceae: <i>Platanus occidentalis</i>	Sycamore	23 Mar (4)	17 Mar (14)		
Fagaceae: <i>Quercus stellata</i> ^b	Post oak	17 Mar (4)	19 Mar (51)		
Fagaceae: <i>Quercus muhlenbergii</i> ^b	Chinquapin oak	4 Apr (2)	17 Mar (2)		
Betulaceae: <i>Betula nigra</i>	River birch	25 Mar (8)			
Cornaceae: <i>Cornus drummondii</i> ^a	Rough dogwood	23 Mar (3)			
Fagaceae: <i>Quercus nigra</i> ^b	River oak	23 Mar (5)	24 Mar (11)		
Juglandaceae: <i>Carya texana</i> ^b	Black hickory	23 Mar (10)	27 Mar (7)		
Ulmaceae: <i>Ulmus crassifolia</i> ^b	Cedar elm		27 Mar (5)		
Fagaceae: <i>Quercus rubra</i> ^b	Red oak		27 Mar (3)		
Fabaceae: <i>Robinia pseudoacacia</i> ^a	Black locust			23 Mar (5)	27 Mar (3)
Sapotaceae: <i>Bumelia lanuginosa</i> ^a	Chittamwood			25 Mar (5)	
Bignoniaceae: <i>Catalpa speciosa</i> ^a	Catalpa			28 Mar (4)	29 Mar (2)
Fagaceae: <i>Quercus macrocarpa</i> ^b	Bur oak	28 Mar (2)			
Salicaceae: <i>Salix nigra</i>	Black willow	4 Apr (8)	27 Mar (9)		
Oleaceae: <i>Fraxinus americana</i> ^b	White ash	2 Apr (3)	27 Mar (4)		
Ulmaceae: <i>Celtis occidentalis</i> ^b	Hackberry	2 Apr (2)	27 Mar (3)		
Anacardiaceae: <i>Toxicodendron radicans</i> ^a	Poison ivy			6 Apr (11)	31 Mar (10)
Juglandaceae: <i>Juglans nigra</i> ^b	Black walnut	8 Apr (4)	31 Mar (10)		
Bignoniaceae: <i>Campsis radicans</i> ^a	Trumpetvine			6 Apr (3)	4 Apr (3)
Fabaceae: <i>Gleditsia triacanthos</i> ^a	Honey locust				7 Apr (6)
Moraceae: <i>Maclura pomifera</i> ^b	Bois-d'arc				8 Apr (41)
Sapindaceae: <i>Sapindus drummondii</i> ^a	Soapberry		8 Apr (5)		
Ulmaceae: <i>Celtis laevigata</i> ^b	Sugarberry	16 Apr (8)	9 Apr (13)		
Juglandaceae: <i>Carya illinoensis</i> ^b	Pecan	20 Apr (10)	10 April (40)		
Ebenaceae: <i>Diospyros virginiana</i> ^{a,b}	Persimmon				11 Apr (27)

^aAnimal pollination; others wind or unknown

^bRing-porous wood; others diffuse-porous

Table 1. Average budburst dates of temperate and tropical species in northern Oklahoma (Tulsa, 36° N) and southern Oklahoma (Durant, 34° N). Number of trees sampled in parentheses.

results. The last species to burst its buds, the pecan, comes from a family of temperate, not tropical, origin, and is represented by numerous individuals in these data sets (Table 1); even though the pecan did not appear to fit the expected evolutionary pattern, the analysis of the entire data set still confirmed the expected pattern. The full story of spring budburst times is very complex, and this paper describes an attempt to look for a broad pattern. There are obviously many exceptions, but a successful evolutionary hypothesis would provide a reliable basis to explain variations in budburst dates in these species and provide general principles for patterns in species not yet studied — as well as potential explanations for those exceptional species, like the pecan, that depart from the general evolutionary expectations.

Each spring, warm temperatures travel north, and tree and shrub buds burst, but some of the trees and shrubs, vestiges of the ancient tropics, still look southward towards their origins, innocently retracing their evolutionary history. Lay people and schoolteachers can observe, measure, and analyze this evolutionary pattern — and, we hope, understand how and why scientists use evolutionary theory in modern biological sciences. Darwin observed these differences in budburst time, within and between tree species, but because he lived at a time of ignorance about continental drift and of the times and places of origin of the several plant families, he perhaps could not have imagined such a quiet vindication of this theory.

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AUTHOR'S ADDRESS

Stanley Rice
Department of Biological Sciences
Southeastern Oklahoma State University
Durant OK 74701-0609
srice@sosu.edu

RUSHDIE ON CREATIONISM

In his novel *The Satanic Verses* (New York: Viking, 1988), Salman Rushdie paints a memorable portrait of a creationist, Eugene Dumsday:

"I am a man of science, sir, and it has been my mission, my mission and let me add my privilege, to visit your great nation to battle with the most pernicious devilment ever got folks' brains by the balls."

"I don't follow."

Dumsday lowered his voice. "I'm talking monkey-crap here, sir. Darwinism. The evolutionary heresy of Mr Charles Darwin." His tones made it plain that the name of anguished, God-ridden Darwin was as distasteful as that of any other forktail fiend, Beelzebub, Asmodeus, or Lucifer himself. "I have been warning your fellow-men," Dumsday confided, "against Mr Darwin and his

works. With the assistance of my personal fifty-seven-slide presentation. I spoke most recently, sir, at the World Understanding Day banquet of the Rotary Club, Cochin, Kerala. I spoke of my own country, of its young people. I see them lost, sir. The young people of America: I see them in their despair, turning to narcotics, even, for I'm a plain-speaking man, to pre-marital sexual relations. And I said this then and I say it now to you. If I believed my great-granddaddy was a chimpanzee, why, I'd be pretty depressed myself" (p 75-6).

Elsewhere, in a review of Malise Ruthven's *The Divine Supermarket: Shopping for God in America* (New York: Arbor House, 1989), Rushdie writes, "Some years ago in South India I encountered the curious and unforgettable figure of Duane Gish, an American creation-

ist scientist whose lectures were accompanied by a jolly slide show: when a slide of a chimpanzee came up, he'd say, 'Oops, that's my grandfather.' Gish gave me the model for the character of Eugene Dumsday in *The Satanic Verses*..." Rushdie's review was reprinted in his *Imaginary Homelands: Essays and Criticism 1981-1991* (London: Granta Books, 1991), p 368-70. That Rushdie found Gish unforgettable is clear from his 1999 essay "Darwin in Kansas" (reprinted in his *Step Across This Line: Collected Nonfiction 1992-2002* [New York: Random House, 2002], p 280-2), in which he again recounted his experience with Gish: "I was interested to note that a few minutes into the lecture the habitually courteous Indian audience simply stopped listening. The hum of conversation gradually rose until the speaker was all but drowned. Not that this stopped Duane. Like a dinosaur who hasn't noticed he's extinct, he just went bellowing on."