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Cover Photograph:

Photographs of a zebra finch, (*Poephila quttata castonotis*) upper left, Owl finch (*P. bicheniovii*) upper right and an interspecific hybrid (bottom center).

Photo Credit: J. L. Wadsworth.

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Journal of the Alabama Academy of Science, Vol. 73, No. 1, January 2002.

PHYLOGENETIC ANALYSIS OF FOUR ESTRILDID FINCH SPP. AND AN INTERSPECIFIC HYBRID

Benjie G. Blair, Mark Meade, Stacy L. Blair

Department of Biological Sciences
Jacksonville State University
Jacksonville, AL 36265

ABSTRACT

The phylogenetic relationships among four species of Estrildid finches, *Poephila quttata castonotis*, *P. bicheniovii*, *P. acuticauda* and *Chloebia gouldiae*, were examined using domestic populations. Crossing a male *P. bicheniovii* with a female *P.q. castopnotis* generated an interspecific hybrid. The hybrid exhibits a combination of morphological and behavioral characteristics common to both parent species. The hybrid responds to the call of either parent. Hybrid progeny were at least partially sterile. Starch gel electrophoresis was employed in order to gain insight into the evolutionary relationships of the four species. Data from five enzyme systems revealed typical segregation of the hybrid progeny. Additionally, the results indicate that the gouldian finch, *C. gouldiae* actually is phylogenetically more related to the zebra finch, *P. q. castonotis*, and the owl finch, *P. bicheniovii* than to the shafttail finch, *P. acuticauda.* Thus, the classification of *C. gouldiae* into a monotypic genus may be unfounded.

INTRODUCTION

Speciation generally occurs when populations of the same species become separated and isolated by a physical barrier. Should the species barriers be removed at a later time, interspecific hybrid potential increases. In cases of fertile hybrids, gene flow between populations becomes a possibility. However, even the sterile hybrids can often provide insight into the genetic composition of (parental) populations and their phylogenetic relationships (Cooke and Buckley, 1987; Landry, 1997).

In the case of the estrildid finch populations, the barrier to population interaction was based on limited water supplies throughout the interior of the Australian continent. As human populations in Australia increased, the landscape of the interior was modified to provide water supplies for cattle and farming. Zebra finch (*P. q. castonotis)* populations increased rapidly resulting in the overlap of geographical ranges among the four species (Goodwin, 1982). The first goal of this study was to examine two domestic populations of estrildids, the zebra and owl finches, and their interspecific hybrid. The study was later expanded to include the estrildid gouldian finch belonging to the monotypic genus *Chloebia* (Goodwin, 1982), and the shaftail finch or "long-tailed" finch, *P. acuticauda.*

Color mutations occur in domestic populations of both the zebra and gouldian finches. As a result of the tremendous range of color variations in these finches, their plumage genetics has been the most studied of any avian species (Aschenborn, 1990; Bates and Busenbark, 1970; Cooke and Buckley, 1987).

The Family Estrildidae

The Family Estrildidae (Order Passeriformes) represents a relatively recent and successful avian evolutionary adaptation (Goodwin, 1982). Today, over 30 genera of estrildid finches occupy a wide variety of ecological niches, from desert environments to tropical forests, across North Africa, Asia and Australia.

Typically, estrildid finches are characterized by their behavior rather than by their morphology. Estrildid finches exhibit strong pair-bonding, especially in cooperative nesting behavior and the care of young. They characteristically build an unwoven covered nest and produce oval, unmarked white eggs. The nestlings typically exhibit conspicuous gape markings or tubercles inside their mouths until well after weaning. They tend to clump between pairs and within flocks where allo-preening occurs in most species. Their diet primarily consists of grass seeds, although a few species have become adapted to feeding on insects and particular types of seeds (Goodwin, 1982; Immelman, 1965; Zann, 1975).

MATERIALS AND METHODS

Feather Collection and Preparation

Plucking several mature feathers induced new or blood feather regeneration. Blood feathers were disinfected with an alcohol swab and transported in 10 ml of calcium and magnesium free phosphate buffer containing 10% fetal calf serum and 100 units each of Penicillin, Streptomycin and Mycostatin on ice. Feather pulp obtained in this manner was stable for about 12 hours before enzyme denaturation was evident. Extraneous pigmented feather material was removed from around the shaft to minimize any material that could interfere with analysis or contribute to microbial contamination (Marsden and May, 1984). An intact shaft containing feather pulp was placed in 0.05 M Tris-HCl buffer adjusted to pH of 7.1 with 1% of each polyvinylpyrrolidone (PVP-40) and mecaptoethanol. A ground glass rod was used to homogenize the shaft and the tissue was immediately frozen –20 ° C. Extraction of these small feathers was performed in the wells of a microtiter plate (96 well).

Starch Gel Electrophoresis

Starch gel electrophoresis and analysis of enzymes were carried out according to the protocol described by Stuber *et al.* (1988). All gels were run anodally with an ice pack placed on the gel surface to reduce thermal deactivation of the enzymes. Of the enzyme systems initially assayed, alcohol dehydrogenase (ADH); lactate dehydrogenase (LDH); malate dehydrogenase (MDH); phosphohexose isomerase (PHI/PGI); and 6-phosphogluconate dehydrogenase (6-PGD) resolved consistently. Either tris-citrate or borate/tris-citrate gel and electrode buffer systems were used.

Sample sizes varied between each species due to availability. The largest sample was of the zebra finches from which 37 individuals were assayed for MDH, LDH, and PHI while only 20 were used for the 6-PGD and the ADH assays. Fifteen owl finches were assayed for MDH, LDH, and PHI. The other systems, 6-PGD and ADH, included only three of the owl finches as samples. All five enzyme systems were assayed in all five interspecific hybrids. A total of eight gouldian finches were assayed for MDH, LDH and PHI included both naturally occurring color morphologies (i.e. black headed and red headed), while three of the eight were assayed for 6-PGD and ADH. Eight shafttail finches were assayed for MDH, LDH, and PHI, while only three of the eight were assayed for 6-PGD and ADH. Even though most of these sample sizes are small, it was felt that they were still representative of the domestic populations in the Southeastern United States. No wild finches have been imported from Australia since 1986. Furthermore breeders exchange birds to the extent that there is one breeding population for each species throughout the Southeast.

Genotypic and allelic frequencies were calculated for each putative locus in each species and the hybrid (Table 1, 2 and 3). The heterozygosity for each species was calculated by averaging over all loci. The genetic distances were calculated by utilizing the coefficient of the kinship equation by Jacquard (1974). Genetic distances were calculated for all pair-wise comparisons of the four species. The distance values were used to construct a dendrogram of the four species.

Table 1. Genotypic Frequencies for 6-pgd

Species/Hybrid	4:4	2:2	6:6	2:4	2:6	2:8	4:6
P.q. castonotis	0.3	0.3	0.05	0.1	0.1	0.1	0.05
P. bicheniovii	0.0	0.0	0.0	1.0	0.0	0.0	0.0
P.q. castonotis X *P. bicheniovii*	0.0	0.0	0.0	1.0	0.0	0.0	0.0
P. acuticauda	0.0	0.0	1.0	0.0	0.0	0.0	0.0
C. gouldiae	0.0	1.0	0.0	0.0	0.0	0.0	0.0

Table 2. Genotypic Frequencies for phi, ldh, mdh and adh

Genotype frequency	phi			ldh	mdh	adh
	7:7	4:7	2:2	4:4	4:4	4:4
P.q. castonotis	0.6	0.36	0.04	1.0	1.0	1.0
P. bicheniovii	1.0	0.0	0.0	1.0	1.0	1.0
P.q. castonotis X *P. bicheniovii*	1.0	0.0	0.0	1.0	1.0	1.0
P. acuticauda	0.77	0.12	0.0	1.0	1.0	1.0
C. gouldiae	0.54	0.46	0.0	1.0	1.0	1.0

Table 3. Allele Frequency for phi, ldh, mdh, adh and 6-pgd

Allele # for	phi			ldh	mdh	adh	6-pgd			
	2	4	7	4	4	4	2	4	6	8
P.q. castonotis	0.04	0.18	0.78	1.0	1.0	1.0	0.45	0.38	0.0	0.05
P. bicheniovii	0.0	0.0	1.0	1.0	1.0	1.0	0.0	1.0	0.0	0.0
P.q. castonotis X *P. bicheniovii*	0.0	0.0	1.0	1.0	1.0	1.0	0.5	0.5	0.0	0.0
P. acuticauda	0.0	0.06	0.94	1.0	1.0	1.0	0.0	0.0	1.0	0.0
C. gouldiae	0.0	0.23	0.77	1.0	1.0	1.0	1.0	0.0	0.0	0.0

RESULTS AND DISCUSSION

Regeneration occurred normally in 14 days with one exception. The interspecific hybrids regenerated feathers within just seven days. This phenomenon could be attributed to a higher metabolic rate associated with "hybrid vigor".

Of the 15 enzyme systems assayed, 5 produced consistent results and were used for the analysis of the relationship of the four finch species and the interspecific hybrid. Discussion and interpretation of the enzyme banding patters have been separated into two groups: a) monomorphic and b) polymorphic enzymes. The monomorphic enzymes include ADH, LDH and MDH, all of which produced identical banding patterns regardless of the taxon tested. The polymorphic enzymes included PHI and 6-PGD. Phosphohexose Isomerase (PHI) is reported to be a dimeric enzyme involved in glycolysis (Cooke and Buckley, 1987). In some individuals PHI produced a two-banded pattern: a densely staining band migrating an average distance of 16 mm and a much fainter band migrating an average distance of 24 mm. Other individuals produced a three-banded pattern: a moderately staining band migrating an average of 16 mm, a darker band migrating an average distance of 27 mm, and a moderately staining band migrating an average distance of 32 mm. Two individuals produced an alternative one-banded pattern. 6-Phosphogluconate dehydrogenase (6-PGD) is also reported to be a dimeric enzyme involved in the pentose shunt (Cooke and Buckley, 1987). Three different one-banded patterns were observed: a moderately staining band migrating an average distance of 20 mm; a densely staining band migrating an average distance of 25 mm; and a darkly staining band migrating an average distance of 30 mm. Three different three-banded patterns were observed and characterized by the following migration rates: 20, 22, and 25 mm; 20, 25 and 30 mm; and 13, 21 and 30 mm. For all of the three-banded patterns the center band was the more densely staining band. One two-banded pattern was observed and characterized by a band migrating 30 mm and a band migrating an average distance of 26 mm. These patterns are interpreted as the phenotypic expression of one locus (6-pgd) which possesses four alleles across all species (Cooke and Buckley, 1987). Previous studies have shown only two of 20 avian taxa to be polymorphic for 6-PGD (Cooke and Buckley, 1987).

Genetic Diversity

The zebra finches used in this study proved to have a greater polymorphism relative to reports of other avian taxa. Forty percent of the loci sampled in zebra finches were polymorphic. Only four of the 92 avian species have previously been shown to have similar polymorphism. Since only domestic populations were sampled and the resulting values of genetic diversity (alleles per locus and percent polymorphism) were unexpectedly high, one might expect even greater diversity in wild populations.

Species Relationships

Using the coefficient of kinship (Jacquard, 1974) the two most closely related species were the owl and zebra finches (Table 4). The two most distantly related were the gouldian and shafttail finches. Because the owl and zebra finches were the most closely related, their allele frequencies were pooled and a second matrix of coefficients of kinship was calculated (Table 5). This clustering procedure is called the unweighted pair-group method of arithmetic averages (Sokal and Sneath, 1963). The dendrogram (Figure 1) constructed suggests that the gouldian finch is more closely related to the owl and zebra finches than is the shafttail finch. This result does not support the continued classification of gouldian finches into the monotypic genus *Chloebia*. It does support their inclusion in the genus *Poephila*.

**Table 4. Coefficients of kinship for each pair of species—
A Distance Matrix**

	1.	2.	3.	4.
1. Zebra				
2. Owl	0.029			
3. Shafttail	0.117	0.095		
4. Gouldian	0.048	0.147	0.158	

Table 5. Coefficients of kinship for each pair of clusters (owl + zebra cluster, Gouldian cluster a Shafttail cluster) - - A distance matrix

	Owl + zebra	Gouldian	Shafttail
Owl + zebra			
Gouldian	0.00031		
Shafttail	0.0155	0.158	

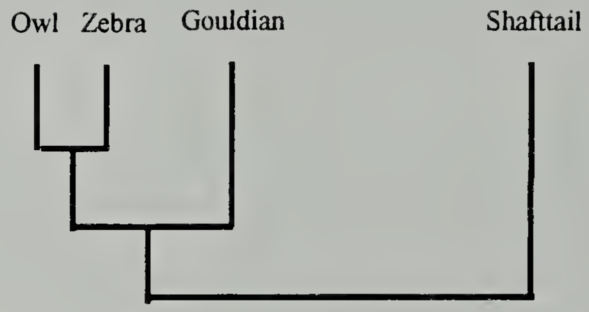

Figure 1. Dendrogram showing the estimated relationship among four species of Estrildid finches, *Poephila quttata castonotis*, *P. bicheniovii*, *P. acuticauda* and *Chloebia gouldiae*.

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A CLIMATOLOGY OF TROPICAL CYCLONE ACTIVITY IN ALABAMA: 1886-1999

Philip L. Chaney, Ph.D.
104 A Tichenor Hall
Department of Geology and Geography
Auburn University, AL 36849
334-844-3420
chanepl@auburn.edu

ABSTRACT

This study investigated the basic characteristics of tropical cyclone activity (i.e., tropical storms and hurricanes) in Alabama in order to provide a greater understanding of the potential threat these natural hazard events pose to Alabama residents and their economic activities. The results indicate 72 tropical cyclones crossed Alabama's borders during the period 1886-1999. Fifteen were classified as hurricanes (65 knots or greater), 36 were tropical storms (35-60 knots), and 21 were tropical depressions (30 knots or less). Seven of the 15 tropical cyclones that made landfall along the Alabama Coast were hurricanes at landfall. The most intense hurricane at landfall was Frederic in 1969 (115 knots). The longest duration in Alabama was 90 hours (3.75 days), but most tropical cyclones crossed Alabama in 24 hours or less. The peak month for cyclone activity in Alabama was September. The decadal frequency of tropical cyclones in Alabama varied considerably, but the average frequency per decade was considerably higher during the period 1886-1939 (8.3) than during the period 1940-1999 (4.5). Furthermore, the total number of tropical cyclones that produced hurricane force winds in Alabama was considerably higher during the period 1886-1939 (10) than during the period 1940-1999 (5).

INTRODUCTION

Tropical cyclones (Table 1) are one of the most destructive natural hazards in Alabama and the Southeastern U.S. (Canis et al. 1985; Monmonier 1997; Bush et al. 2001). Two of the most infamous examples of the catastrophic damage that Alabama residents have experienced from tropical cyclones were the impacts of Hurricane Frederic in 1979 and Hurricane Opal in 1995. Frederic made landfall at Dauphin Island, Alabama, and caused 10 deaths and approximately $1.4 billion in damages (Parker et al. 1993). Opal made landfall near Pensacola, Florida, then tracked across Alabama where it left 6 dead and approximately 38 counties in need of disaster relief (National Climatic Data Center 1995). These examples demonstrate the threat that tropical cyclones represent to Alabama's residents and their economic activities (e.g., agriculture, forestry, fishing, tourism, and shipping). Furthermore, these examples show that a tropical cyclone's damage is not limited to the coast, or to the state where it made landfall. This first point is especially significant because tropical cyclones are generally perceived as a coastal hazard; however, they also represent a significant threat to inland areas in the form of high wind speeds, floods, and tornadoes (Monmonier 1997; Pielke and Pielke 1997). Therefore, a review of the historical record was undertaken to identify the basic characteristics of tropical cyclone activity across the entire state of Alabama (i.e., frequency, intensity, and duration), and to identify trends or patterns that may provide a better understanding of tropical cyclone activity for future planning and management purposes.

Table 1. Tropical cyclone intensity scale (based on Simpson 1974 and National Oceanic and Atmospheric Administration 1977).

Tropical Cyclone Class	Saffir/Simpson Category	Central Pressure (mb)	Wind Speed (mph)	Wind Speed (knots)
Tropical Depression	---	---	≤ 38	≤ 33
Tropical Storm	---	---	39-73	34-63
Hurricane	1	≥ 980	74-95	64-82
Hurricane	2	965-979	96-110	83-95
Hurricane	3	945-964	111-130	96-113
Hurricane	4	920-944	131-155	114-135
Hurricane	5	<920	>155	>135

DATA AND METHODS

HURDAT (Best Tracks)

The tropical cyclone database used in this study is officially known as HURDAT (hurricane database) and is maintained by the National Hurricane Center (2000). The HURDAT database consists primarily of 6-hour interval observations on storm center positions (latitude and longitude, in tenths of degrees) and wind speeds (knots, in 5-knot intervals) for tropical cyclones observed in the North Atlantic Basin dating back to 1886. The HURDAT database is based on Greenwich Mean Time (GMT); therefore, the 6-hour interval observations are recorded at GMT 00:00 hours, 06:00 hours, 12:00 hours, and 18:00 hours. The HURDAT database is more commonly known as "best tracks" because the storm positions represent the best estimate of the eye of the cyclone as determined from sources such as ship observations, land station observations, aircraft surveillance, and satellite monitoring (Jarvinen et al. 1984). The best tracks database is recognized as the primary source for historical studies of tropical cyclone activity in the Atlantic region (Neumann and McAdie 1997); however, it should be noted that data collected before aerial reconnaissance became routine in 1944 may not be as complete as the more recent data (Jarvinen et al. 1984). A detailed description of the history and format of the database is available in Jarvinen et al. (1984), and noteworthy discussions are available in Neumann et al. (1993), Neumann and McAdie (1997), Elsner and Kara (1999), and Landsea (1993).

Storm Track Definitions and Analysis

The method to determine which tropical cyclones qualified as having been officially observed in Alabama consisted of plotting the 6-hour interval storm center positions recorded in the best tracks database, plotting the lines that connected the storm center positions (i.e., storm tracks), and then selecting only those tracks that intersected the state boundaries of Alabama. The state boundary map of Alabama used to evaluate the storm tracks was obtained from the NOAA Coastal Services Center (2000). The southern extent of Alabama's physical boundary is not clearly defined because it consists of land (Morgan Peninsula and Dauphin Island) and open water (Mobile Bay and Petit Bois Pass); therefore, a line approximating a continuous, east-west shoreline across the open water sections was used to determine the location and time of landfall. Since Alabama's western boundary extends through Mississippi Sound, the same methodology was applied in that a tropical cyclone was considered to be in Alabama when it crossed the state boundary line that extends through Mississippi Sound, as opposed to waiting till a storm center position was recorded over land. Tropical cyclones that entered Alabama by crossing this section of the western boundary (via Mississippi Sound) were considered to have made landfall in Mississippi, not Alabama.

For each tropical cyclone, the point of origin was defined as the first storm center position recorded in the best tracks database, which is consistent with the method used by Vega and Binkley (1993). The date of origin was defined as the date of the first position recorded in the best tracks database. The maximum wind speed was defined as the highest wind speed observation associated with a storm center position recorded within the state's boundaries. Tropical cyclones with storm tracks that crossed a corner of Alabama, but were not over the state long enough for a 6-hour interval storm center position to be recorded within the state's boundaries, were assigned the wind speed associated with the last position recorded in the database before the tropical cyclone crossed into Alabama. The wind speed of a tropical cyclone at the time of landfall was defined as the wind speed associated with the last position recorded over the Gulf of Mexico before landfall. This definition is based on the tendency for a tropical cyclone to decrease in intensity (wind speed) as it passes over land as a result of frictional factors and isolation from the source of energy (warm ocean water) (Dunn and Miller 1964; Elsner and Kara 1999). The date of landfall was defined as the date of the last position recorded before landfall, which was defined as the official observation for determining wind speed at landfall.

The length of time that a tropical cyclone was over Alabama (i.e., duration) was defined as the number of 6-hour interval storm center positions recorded within the state's boundaries. The error associated with this method is within +/- 6 hours (i.e., +/- one 6-hour interval observation). For example, a tropical cyclone with 2 storm center observations in Alabama was assigned a duration of 12 hours; however, the actual duration may have varied from slightly over 6 hours to slightly under 18 hours. Tropical cyclones with storm tracks that crossed a corner of Alabama, but were not over the state long enough for a 6-hour interval storm center position to be recorded within the state's boundaries, were assigned a duration of less than 6 hours.

Lastly, regression analysis was used to evaluate the temporal relationship between the frequency of tropical cyclones observed in Alabama and the frequency of tropical cyclone development in the North Atlantic Basin (Gulf of Mexico, Caribbean Sea, and the North

Atlantic Ocean). The tropical cyclone frequency data were sorted by decade, and then the analysis was conducted with the Alabama data serving as the dependent variable (y) and the North Atlantic Basin data serving as the independent variable (x) (Rogerson 2001).

RESULTS

Frequency of Tropical Cyclones in Alabama

A total of 72 tropical cyclones were observed in Alabama during the period 1886-1999 (Figure 1). These storms accounted for approximately 7.45% of the 966 tropical cyclones observed in the North Atlantic Basin during the study period. The earliest date of origin for a tropical cyclone observed in Alabama was May 28th (1959), and the latest date of origin was October 29th (1904). The month of origin that produced the highest frequency of tropical cyclones observed in Alabama was September (25 of 72; 34.72%) (Figure 2). The region that produced the highest percentage of Alabama tropical cyclones was the Atlantic Ocean (30 of 72; 41.67%), followed by the Caribbean Sea (21 of 72; 29.17%), Gulf of Mexico (19 of 72; 26.39%), and Pacific Ocean (2 of 72; 2.77%). Note that 4 tropical cyclones actually originated in the eastern Pacific and then migrated into the Atlantic, region where 2 hit Alabama.

The annual frequency of tropical cyclones observed in Alabama during the 114-year study period was 0.63 (i.e., 63 per 100 year interval); therefore, the return period of tropical cyclones in Alabama was 1.58 years. The longest period of consecutive years in which a tropical cyclone was observed in Alabama was 6 years (1991-1996), and the longest period of consecutive years in which no tropical cyclones were observed in Alabama was 7 years (1940-1946) (Figure 3). The decadal frequency of tropical cyclones observed in Alabama varied considerably with the highest frequency (12) in the 1910s and the lowest frequency (3) in the 1940s and 1980s (excluding the 1880's when the record was incomplete) (Figure 4A). Although the decadal frequency of tropical cyclone development in the North Atlantic Basin also varied considerably (Figure 4B), the temporal relationship between the decadal frequency of tropical cyclones observed in Alabama and the decadal frequency of tropical cyclone development in the North Atlantic Basin was weak (correlation coefficient = 0.20; r square = 0.04) (Figure 5).

Frequency of Alabama Landfalls

Fifteen of the 72 tropical cyclones observed in Alabama made landfall along the Alabama Coast, which accounted for 20.83% of the Alabama storms (Table 2). Note that 2 of those 15 tropical cyclones made an initial U.S. landfall along Florida's Atlantic Coast before entering the Gulf of Mexico, and 4 made an initial U.S. landfall along the Louisiana Coast near the mouth of the Mississippi River. The annual frequency of tropical cyclones that made landfall in Alabama was 0.13, and the return period was 7.69 years. The only period in which Alabama landfalls occurred in consecutive years was 1901-1902, and no single year included multiple (2 or more) landfalls in Alabama. The longest period of consecutive years in which no tropical cyclones made landfall in Alabama was 19 years (1960-1978). The highest frequency of Alabama landfalls occurred in September (6 of 15; 40%); and each major region of origin produced a relatively equal frequency of Alabama landfalls: Atlantic Ocean (5), Gulf of Mexico (5), and Caribbean Sea (4). The remaining tropical cyclones (57 of 72) made landfall along the U.S. Coast from Texas to Georgia and traveled overland to Alabama. The most common locations for those storms to make landfall was the Northwest Florida Panhandle (28), Louisiana (11), and Mississippi (8).

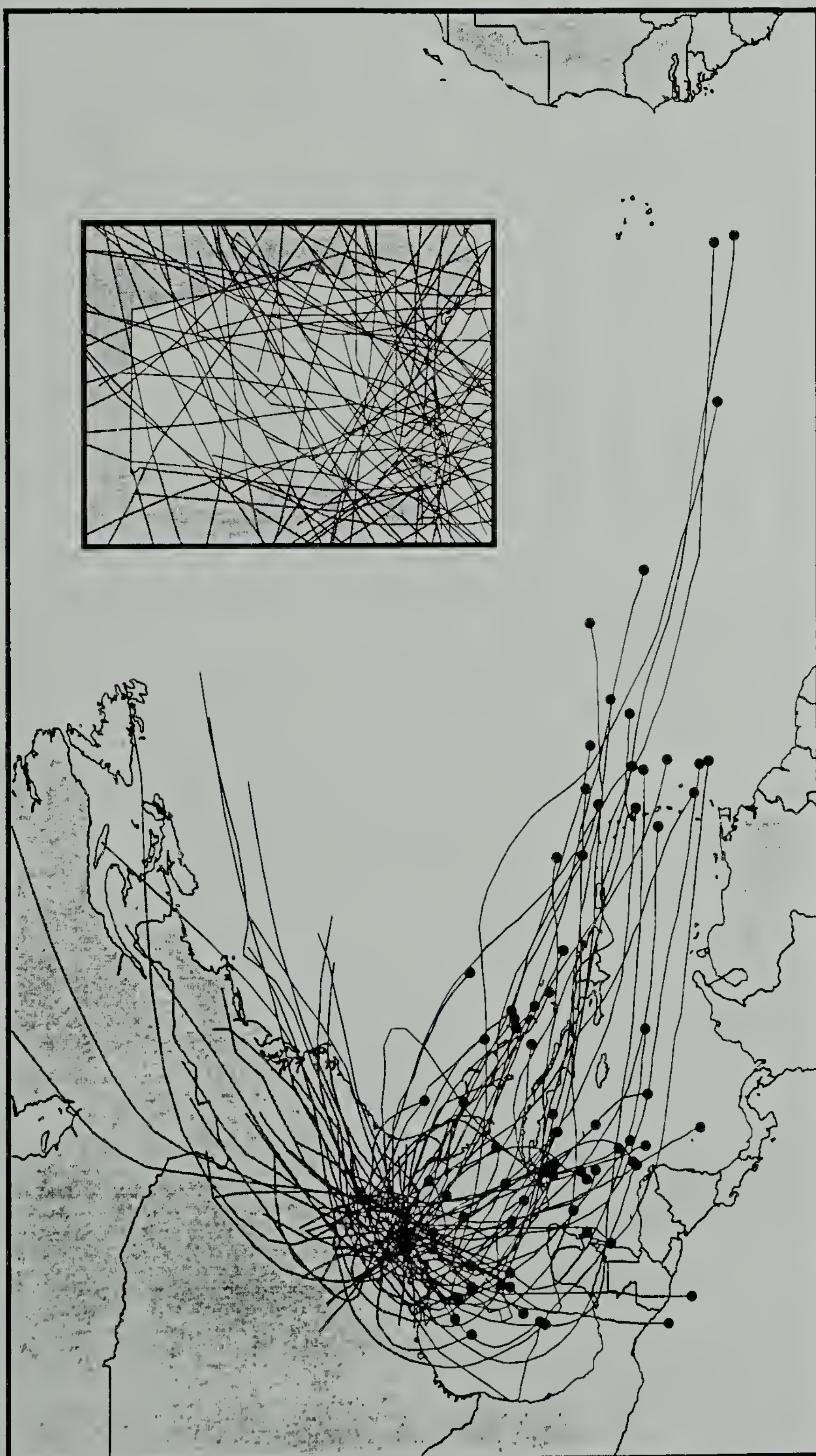

Figure 1. Storm tracks of the 72 tropical cyclones observed in Alabama during the period 1886-1999.

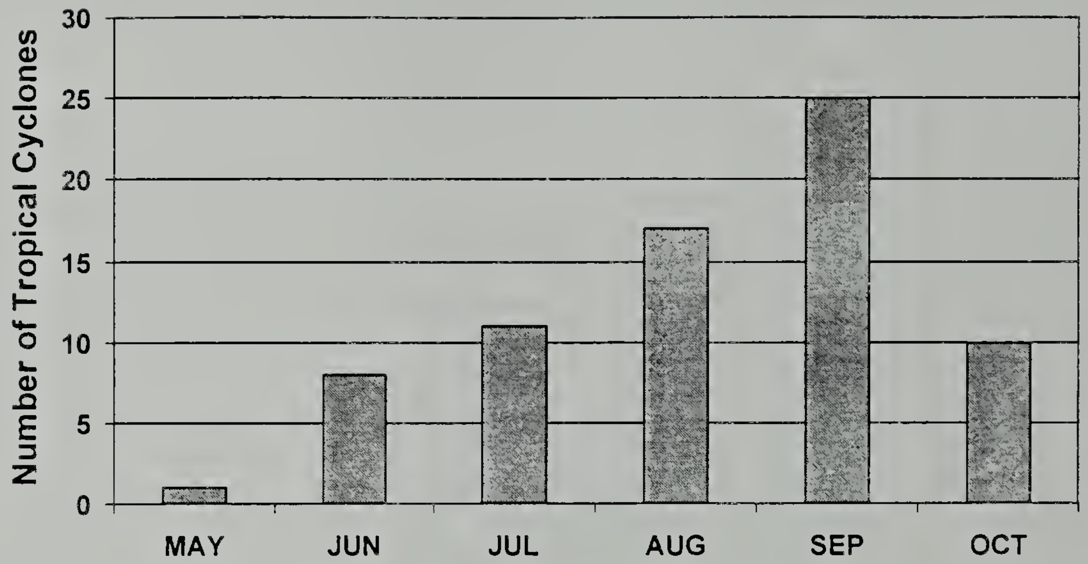

Figure 2. Total number of tropical cyclones observed in Alabama by month for the period 1886-1999.

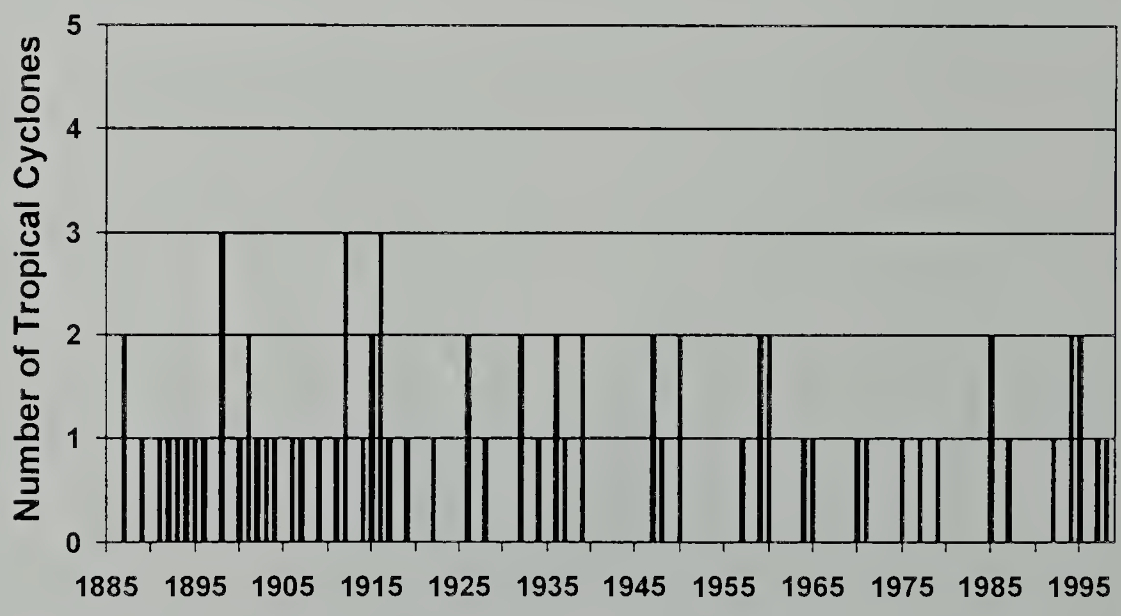

Figure 3. Total number of tropical cyclones observed in Alabama each year during the period 1886-1999.

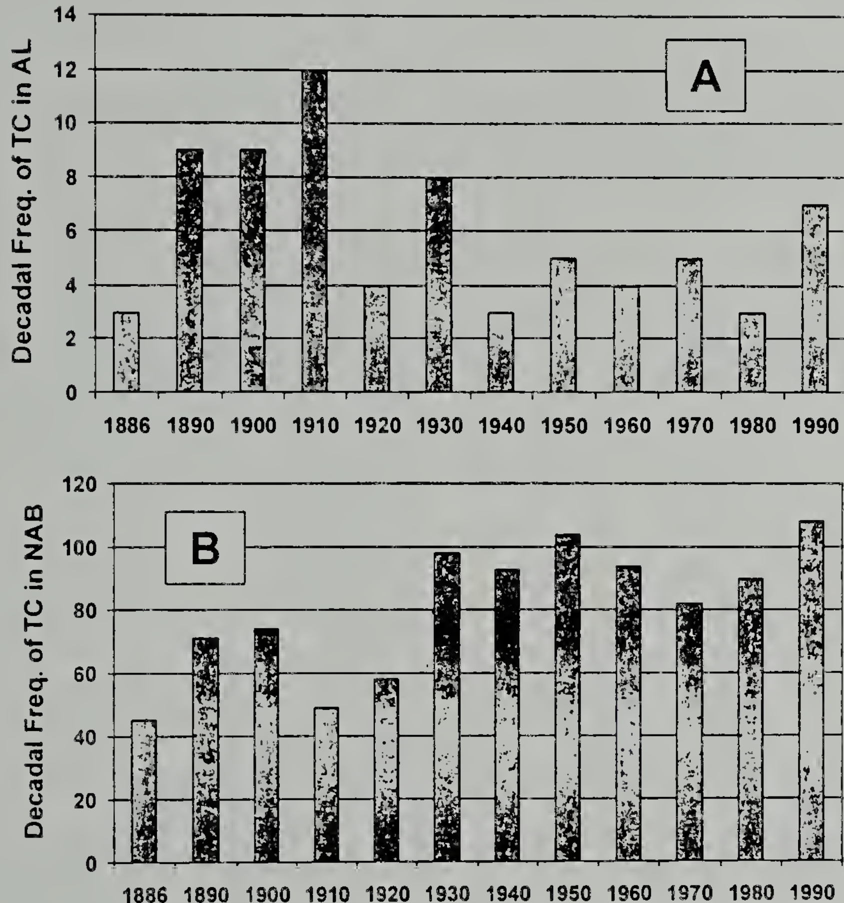

Figure 4. Top chart (A) shows decadal frequency of tropical cyclones observed in Alabama and lower chart (B) shows decadal frequency of tropical cyclone development in North Atlantic Basin during the period 1886-1999 (years listed along x-axis indicate first year of decade).

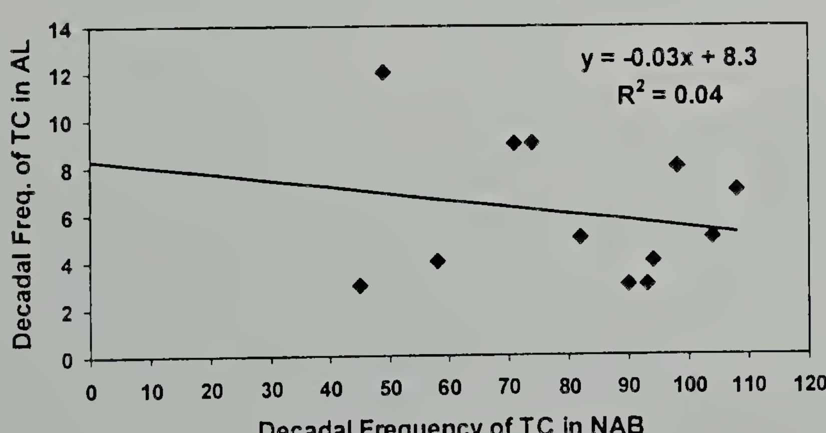

Figure 5. Scatterplot and regression analysis of decadal frequency of tropical cyclone development in North Atlantic Basin (x-axis) and decadal frequency of tropical cyclones observed in Alabama (y-axis) during the period 1886-1999.

Table 2. Tropical cyclones that made landfall along the Alabama Coast during the period 1886-1999. It should be noted that a number of those tropical cyclones made an earlier U.S. landfall before striking the Alabama Coast.

		Origin of Tropical Cyclone			Landfall in Alabama	
Name*		Year	Date (mm/dd)	Region	Date (mm/dd)	Wind Speed (knots)
---	***	1889	9/11	Atlantic	9/23	85
---		1901	6/10	Caribbean	6/14	35
---	***	1902	10/03	Pacific	10/10	50
---		1912	9/11	Gulf of Mexico	9/14	70
---		1922	10/12	Caribbean	10/17	40
---	**	1926	9/11	Atlantic	9/21	95
---	**	1932	8/26	Atlantic	9/01	70
---		1934	10/01	Caribbean	10/06	35
---		1939	6/12	Caribbean	6/16	35
---		1947	9/07	Gulf of Mexico	9/08	35
Baker		1950	8/20	Atlantic	8/31	75
Irene		1959	10/06	Gulf of Mexico	10/08	50
Frederic		1979	8/29	Atlantic	9/13	115
Juan	***	1985	10/26	Gulf of Mexico	10/31	60
Danny	***	1997	7/16	Gulf of Mexico	7/19	70

* Tropical cyclones were not assigned official names until 1950 (Neumann et al. 1993).
** Made initial U.S. landfall along Florida's Atlantic Coast.
*** Made initial U.S. landfall along the Louisiana Coast.

Intensity

Fifteen of the 72 tropical cyclones observed in Alabama (20.83%) produced maximum sustained wind speeds in the hurricane intensity range (64 knots or above; Table 1) while crossing the state (Figure 6). Thirty-six of the 72 tropical cyclones (50%) produced maximum sustained wind speeds in the tropical storm intensity range while crossing the state (34-63 knots), and the remaining twenty-one tropical cyclones (29.17%) produced maximum sustained wind speeds below the tropical storm limit while crossing the state (30 knots or below).

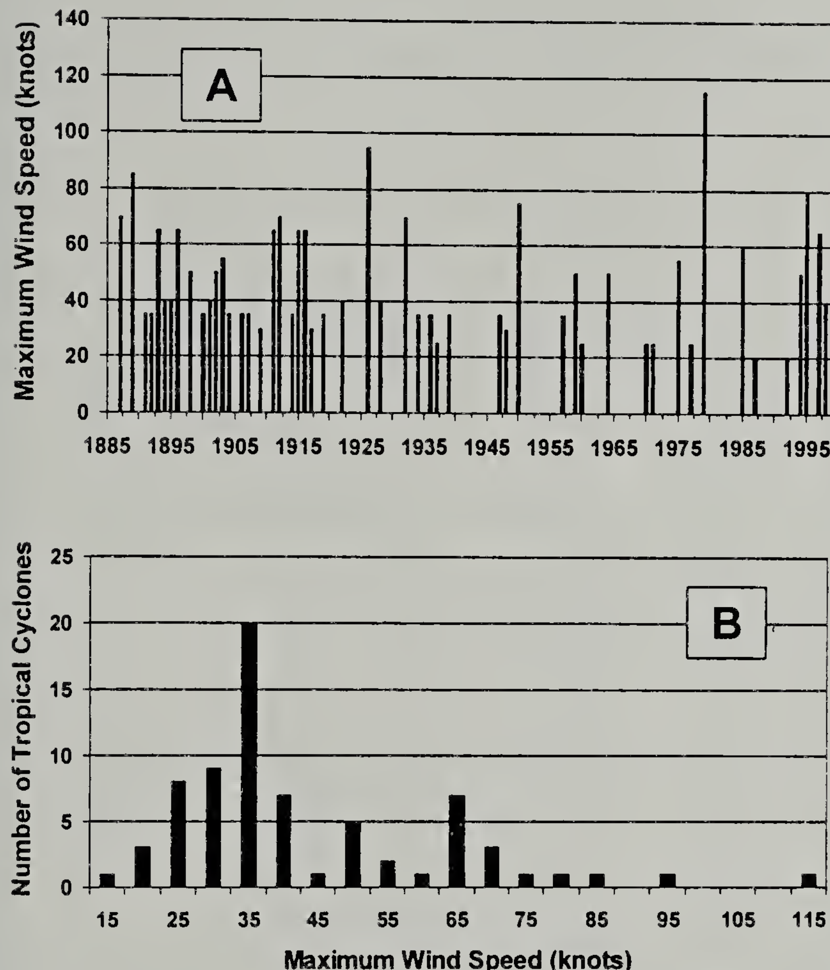

Figure 6. Top chart (A) shows maximum wind speed of most intense tropical cyclone observed in Alabama each year during the period 1886-1999. Lower chart (B) shows histogram of the maximum wind speeds of the tropical cyclones observed in Alabama.

Seven of the 15 tropical cyclones that produced hurricane winds in Alabama made landfall along the Alabama Coast, seven made landfall along the N.W. Florida Coast, and one made landfall along the Mississippi Coast (Table 3). The annual frequency of tropical cyclones that produced hurricane winds in Alabama was 0.13, and the return period was 7.69 years. There were no periods in which tropical cyclones produced hurricane winds in Alabama in consecutive years. However, there was one case in which two tropical cyclones (Erin and Opal) produced hurricane winds in Alabama in a single year (1995). The longest period of consecutive years in which no tropical cyclones produced hurricane winds in Alabama was 28 years (1951-1978). The month in which the highest frequency of tropical cyclones produced hurricane winds in Alabama was September (6 of 15; 40%). The region of origin that produced the highest frequency of tropical cyclones that produced hurricane winds in Alabama was the Atlantic Ocean (7 of 15; 46.67%). The highest sustained wind speed produced by a tropical cyclone in Alabama was 115 knots, which was recorded in Frederic (1979) just before landfall at Dauphin Island. It should be noted, however, that Schramm et al.

(1980) reported that a sustained wind speed of 126 knots was recorded "at the bridge on the Dauphin Island causeway" as Frederic made landfall.

Table 3. Tropical cyclones that produced hurricane winds (65 knots or above) while crossing Alabama during the period 1886-1999.

	Origin of Tropical Cyclone			Landfall		Hurricane Winds in Alabama	
Name*	Year	Date (mm/dd)	Region	Date (mm/dd)	State**	Max. Speed (knots)	Duration (hours)
---	1887	7/20	ATL	7/27	FG	70	6
---	1889	9/11	ATL	9/23	AL (LA)	85	6
---	1893	9/27	CAR	10/2	MS (LA)	65	6
---	1896	7/4	CAR	7/7	FG	65	6
---	1911	8/9	GOM	8/11	FG	65	6
---	1912	9/11	GOM	9/14	AL	70	6
---	1915	8/31	CAR	9/4	FG	65	6
---	1916	10/12	CAR	10/18	FG	65	6
---	1926	9/11	ATL	9/21	AL (FA)	95	6
---	1932	8/26	ATL	9/1	AL (FA)	70	6
Baker	1950	8/20	ATL	8/31	AL	75	6
Frederic	1979	8/29	ATL	9/13	AL	115	<6
Erin	1995	7/31	ATL	8/3	FG (FA)	65	6
Opal	1995	9/27	CAR	10/4	FG	80	6
Danny	1997	7/16	GOM	7/19	AL (LA)	70	12

* Tropical cyclones were not assigned official names until 1950 (Neumann et al. 1993).
**Point of landfall: Alabama (AL), Florida Gulf Coast (FG), Florida Atlantic Coast (FA), Louisiana (LA), and Mississippi (MS). State codes in parentheses indicate location of initial U.S landfall.

Duration

Eight of the 72 tropical cyclones observed in Alabama (11.11%) had a duration period (i.e., length of time the center of the storm was over the state) in excess of 24 hours (Figure 7). Seventeen of the tropical cyclones observed in Alabama (23.61%) had a duration period of approximately 18-24 hours, and 47 tropical cyclones (65.28%) had a duration period of approximately 12 hours or less. The longest duration in Alabama was approximately 90 hours (3.75 days), which was recorded in 1939 as a tropical depression (30 knots or below; Table 1) migrated slowly across the entire state. More importantly, the duration of the hurricane winds in Alabama produced by the 15 tropical cyclones identified earlier in this study (Table 3) was limited to approximately 6 hours or less in each case, except Danny, which produced hurricane winds for approximately 12 hours as it migrated across Mobile Bay.

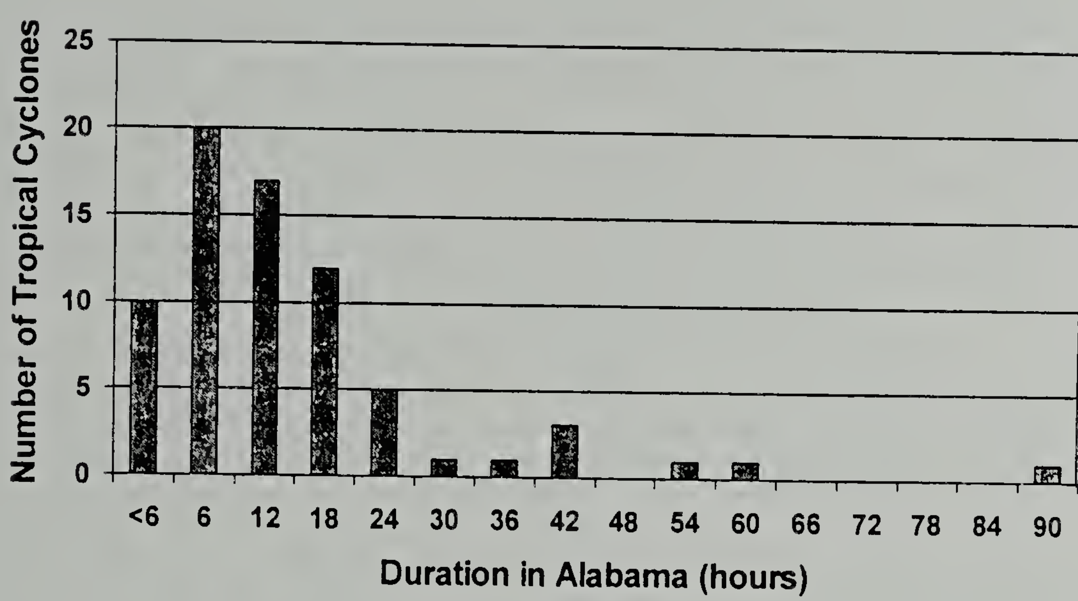

Figure 7. Histogram of the duration of the tropical cyclones observed in Alabama during the period 1886-1999,

DISCUSSION

Tropical cyclones were observed across the entire state of Alabama during the study period (Figure 1), and there was considerable variability in frequency, intensity, and duration. In regard to the first issue, tropical cyclone frequency in Alabama was relatively high from the beginning of the study period in 1886 through the 1930s (Figures 3 and 4A), declined during the 1940s to 1980s, then returned to slightly above normal in the 1990s (i.e., 6.3 per decade). More specifically, the annual frequency of tropical cyclones in Alabama decreased from 0.83 for the period 1886-1939, to 0.45 for the period 1940-1999, which was a decline of approximately 45.8%. A simple explanation for the trends observed in Alabama during these periods is that there was a direct relationship between tropical cyclone activity in Alabama and tropical cyclone development in the North Atlantic Basin, and therefore, the trends observed in Alabama were simply a reflection of trends in tropical cyclone development in the North Atlantic Basin. However, tropical cyclone activity in the North Atlantic Basin during the study period (Figure 4B) actually increased from an annual frequency of 7.31 (1886-1939) to 9.52 (1940-1999). Furthermore, regression analysis of the decadal frequency of tropical cyclones in Alabama and the decadal frequency of tropical cyclone development in the North Atlantic Basin showed conclusively that the temporal relationship between these two variables was extremely weak (Figure 5).

A related issue on tropical cyclone frequency in Alabama concerns the frequency of years in which tropical cyclones were actually observed in Alabama. Although 72 tropical cyclones were observed in Alabama during the 114-years included in study, tropical cyclones were actually observed in only 52 of those years (Figure 3). More specifically, a single tropical cyclone was observed in 35 years, and multiple (2-3) tropical cyclones were observed in 17 years. Therefore, a tropical cyclone was observed in Alabama in 45.61% of the years included in the study period, which is a return period of approximately 2.19 years. These findings suggest that it might be prudent to also consider tropical cyclone impacts in terms of the frequency of years in which tropical cyclones are actually observed in Alabama, as opposed to focusing on the frequency of individual events. From an emergency services or resource management perspective, it is especially interesting to note the fact that more than 1 tropical cyclone crossed Alabama's borders in approximately 1/3rd (17 of 52; 32.69%) of the years in which a tropical cyclone was observed in Alabama. Furthermore, multiple tropical cyclones were observed in Alabama in consecutive years on three occasions (1915-1916, 1959-1960, and 1994-1995), and the longest period between years in which multiple tropical cyclones were observed in Alabama was 24 years (1961-1984).

In regard to intensity and duration, at the extreme (maximum) end of the spectrum were 15 tropical cyclones that produced hurricane winds in the state (Table 3) and 8 tropical cyclones that had a duration period in excess of 24 hours (Figure 7), both of which would have contributed significantly to the total amount of flooding and/or wind damage from tropical cyclone activity in Alabama. The 15 tropical cyclones that produced hurricane winds while crossing the state accounted for a significant portion of the 72 tropical cyclones observed in Alabama (20.8%), and furthermore, the 7 tropical cyclones that produced hurricane winds at landfall accounted for approximately 45% of the 15 tropical cyclones that made landfall along the Alabama Coast (Table 2).

However, Alabama was fortunate that the duration of the hurricane winds was limited to 6 hours or less in all but one case (Table 3). Furthermore, major hurricanes (Category 3 or above; Landsea 1993) have been shown to be responsible for approximately 80% of tropical cyclone damage in the U.S. (Hebert et al. 1993; Pielke and Landsea 1998), so Alabama was indeed fortunate that only 1 tropical cyclone was a major hurricane at landfall (Frederic in 1979; Table 2). Lastly, 10 tropical cyclones produced hurricane winds in Alabama during the period 1886-1939 (return period = 5.4 years), but only 5 produced hurricane winds in Alabama during the period 1940-1999 (return period = 12.0 years) (Figure 5A). Although closer inspection shows that 3 tropical cyclones produced hurricane winds in Alabama in the 1990s (Table 3), which indicates frequency has increased in recent years, the fact remains that the overall frequency of tropical cyclones that produced hurricane winds in Alabama decreased significantly (-55%) during the later part of the study period.

SUMMARY AND CONCLUSIONS

This study evaluated a historical database on tropical cyclone activity maintained by the National Hurricane Center (2000) and determined that the center of 72 tropical cyclones crossed Alabama's state boundaries during the period 1886-1999. The analyses of those tropical cyclones provide a detailed review of the frequency, intensity, and duration of tropical cyclones that passed directly over Alabama during the study period. It should be noted that the methodology employed in this study excluded tropical cyclones that passed near Alabama's borders and may have had some impact on the state. Therefore, it is recommended that future research address this issue with a methodology that considers tropical cyclone storm tracks within various distances of the state's boundaries (e.g., storm tracks within a 100-mile buffer zone surrounding the state's borders).

Nevertheless, one of the most noteworthy results of this study concerns variability in the frequency of tropical cyclones observed in Alabama, especially when considering the recent findings of Goldenberg et al. (2001) that suggested tropical cyclone development in the North Atlantic Basin will be higher than normal over the next 10-40 years. A natural response to those findings is to assume that tropical cyclone frequency in Alabama will increase accordingly. However, the results of this study clearly showed that the temporal relationship between the decadal frequency of tropical cyclone development in the North Atlantic Basin and the decadal frequency of tropical cyclones observed in Alabama was weak. Although additional research that incorporates the methodology discussed earlier is recommended, the findings of this study do not support the assumption that the projected increase in tropical cyclone development in the North Atlantic Basin over the next few decades (10-40 years) clearly signals an increase in tropical cyclone activity in Alabama over the same period.

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IN VITRO EXTERNAL FACTORS INFLUENCING TIGHT JUNCTIONS AND THE ACCURACY OF TRANSEPITHELIAL ELECTRICAL RESISTANCE MEASUREMENT

John G. Eley

Department of Pharmacal Sciences
Harrison School of Pharmacy
Walker Building, Dormitory Drive
Auburn University, Auburn, AL 36849
E-mail: eleyjoh@auburn.edu

ABSTRACT

Both epithelial and endothelial cells have the ability to control the diffusion of solutes across their membranes by extraordinary complex structures known as tight junctions. Recently these structures that give rise to paracellular transport have been shown to contain a relatively large amount of protein. In vitro tight junction control is usually measured by transepithelial electrical resistance (TEER) across cell monolayers, which indicates junction status as either open or closed. During the course of permeability testing it was observed that the physical movement of cells including laboratory handling coupled with a change in temperature caused immediate inconsistencies in resistance measurement. On standing for various periods cells were observed to regain their original resistance and achieve a steady state condition shown by consistent readings. This initiated a note a caution in that readings taken before cells had reached this consistent state would be inaccurate. The cause of this initial drop in resistance and gradual recovery was investigated and shown to be independent of temperature and influenced by physical movement of cell plates by the fluid pressure produced by the nutrition medium that covers the cells. It was speculated that the effect could be due to the primary extracellular loop of the protein occludin. The vulnerability of this protein to change in fluid pressure and movement could initiate the mechanism for tight junction. A separate observation concerning the use of "chopstick" electrodes concluded that such measurements should be used only for *estimating* resistance.

Key Words: Tight junctions, Cell culture, Occludin

INTRODUCTION

Tight junctions between epithelial and endothelial cells function as barriers to the diffusion of membrane proteins between apical and basolateral areas of membranes. If equilibrium is altered, for example the removal of extracellular calcium ions required for tight junction viability, membrane constituents become disrupted. A second equally important function of tight junctions is to maintain a seal between surrounding cells preventing the leakage of water soluble molecules. (Schneeberger and Lynch, 1992; Gumbiner, 1993) In the absence of functional tight junctions cellular sheets cannot function to maintain homeostasis. Far from being a simple open or closed structure the tight junction, which gives access to cells via the paracellular pathway, has proved to be most complex consisting of some unique proteins. (Tsukita et al.1996; reviews: Tsukita and Furuse, 1999, 2000, 2001).

While conducting permeability enhancement experiments with a series of alkylglycosides using the cell model T-84, difficulties became apparent with respect to measurement of resistance. Change in resistance is an indication of tight junction "leakiness." When the junctions are fully closed the cell monolayer exhibits a high resistance and as they are loosened resistance falls. If recovery is not apparent after the application of an agent to the cell surface it can be assumed that tight junctions were not the only means of transport for the agent. Cell membrane solubilization may occur which can result in irreversible disruption of cell components. It is essential that a steady resistance reading be obtained before measurement is meaningful. It was noted that stress placed upon the cells such as movement from incubator to a biological cabinet (which included a temperature change), or change of medium, would cause resistance readings to become erratic. If left unhindered resistance across the cell monolayers would rise to a reading termed "steady-state" where at least three constant readings were observed after 30-40 minutes. Usually cells that have not been moved before resistance measurement show a requirement to attain a steady state reading. However, this is relatively short compared to the time required to record steady state readings after movement of cell plates. The simple addition of electrodes disturbs cell junctions. Whether it is also cell disturbance that accounts for longer time periods to obtain steady state conditions when the cell plates are moved was not obvious. Therefore it was decided to monitor and record changes in resistance due to movement of cell plates more closely. The aim was to observe cell resistance for reproducible conditions and determine why this phenomenon was occurring. So far as we know this type of cell behavior has not been reported before probably because cells are usually allowed to stand but are not monitored by resistance measurements before data collection begins.

A separate observation thought to be unconnected to tight junction integrity was made when using the STX-2 electrode system for resistance measurement. Fluctuation of resistance measurement was a constant feature of this system; The STX-2 "chopstick" electrodes were found to be unreliable for consistent recordings. Readings would fluctuate considerably and reproducible results were unattainable.

MATERIALS

T-84 cells were purchased from the American Type Culture Collection, (Manassas, VA). All cell culture materials, Hank's balanced salt solution (HBSS), Dulbecco's Modified Eagle Medium (DMEM)/Ham's F-12, Eagles Minimum Essential Medium (E.MEM)/Hank's Balanced Salt Solution (HBSS), heat inactivated fetal bovine serum (FBS), non-essential amino acids (NEAA), trypsin/EDTA solution, and phosphate buffered saline was purchased from HyClone, (Logan, UT). Gentamicin from Sigma (St. Louis, MO). Cell flasks, pipettes, and general cell consumables were purchased from Fisher Scientific, (Atlanta, GA). Transwell® permeable support (cell culture inserts, clear polyester membranes) were purchased form Corning Scientific Products, (Action, MA). All other chemicals and materials were of analytical grade and obtained from Fisher Scientific, (Atlanta, GA).

METHODS

Cell Culture Conditions

T-84, a human adenocarcinoma cell line was obtained at passage number 53 and seeded at 1 x 10^4 cells/ml in $75cm^2$ flask until confluent. Cells were maintained in DMEM/Ham's F-12 supplemented with 5% heat inactivated fetal bovine serum (FBS). All medium contained non-essential amino acids (NEAA) and 0.01% gentamicin. Cells were maintained at 37° C in an atmosphere of 5% CO_2.

Cells were passaged by rinsing with calcium/magnesium free HBSS and addition of 0.25% trypsin/1mM EDTA for 1-1.5 minutes. After aspiration cells were placed in an incubator at 37° C for 15 minutes, when medium was added to detach the monolayer. Cells were reseeded in new flasks at 1 x 10^4 cells/ml. These cells were passaged approximately once every five days depending on their advancement in the log-phase of growth. Medium was changed every 2-3 days. Cells were transferred to permeable polyester filters (surface area $1cm^2$) within Transwell® plates by harvesting from $75cm^2$ flask and seeded at 7.5 x 10^4 cells/ cm^2 after counting on a Coulter Counter Mode Z1 (Mialeah, FL).

Monolayer Integrity

Resistance across the cell monolayers was measured every 24 hr by transepithelial electrical resistance (TEER) after the cells had reached a confluent growth state. The measuring instrumentation consisted of an Evom™ Epithelial voltohmmeter and an Endohm™ tissue resistance measurement chamber, World Precision Instruments, (Sarasota, FL). The voltohmmeter attached to the chamber (capable of accommodating a 6, 12, or 24 mm diameter well) provides reproducible resistance measurements of cell monolayers in culture wells. Wells containing cells were transferred to the Endohm chamber and a cap placed in position. Both chamber and cap each contain a pair of concentric electrodes consisting of a voltage-sensing silver/silver pellet in the center plus an annular current electrode. The height of the top electrode can be adjusted to fit cell culture wells to the correct depth and allow a uniform current density to follow across the well membrane and cell monolayer. Because of the uniform density of the AC square wave, current from the voltohmmeter or membrane capacitance is largely eliminated. EVOM's "chopstick" electrode STX-2 is a fixed pair of double electrodes 4mm wide and 1mm thick. Each stick of the pair contains a silver/silver chloride pellet for measuring voltage and a silver electrode for passing current. The small size of each electrode stick aids its placement into cell culture wells. One electrode is 2.5mm longer than the other in order to fit the deeper outer chamber of the well. High resistance measurements indicated cells were closely packed and forming tight-junctions. Blank calibration wells were used to determine background resistance. Resistance of cell monolayers was determined as resistance minus backgrounds multiplied by the surface area of the insert, in ohm cm^2.

Steady State Resistance Readings

Steady state readings were considered viable when three or more resistance readings were consistent ± 1 Ohm, regardless of the time period to achieve this. Cell plates were either measured by TEER in-situ in an incubator or after transference to a biological safety cabinet. In the latter case cells would be moved from a temperature of 37°C to room temperature. Resistance was measure both across cells maintained in medium with added serum and with medium without serum, as it was reasoned that the protein content may affect resistance readings. For temperature dependent readings resistance was measured remotely with the cells in an incubator. Cells were transferred and measurements taken either as the temperature decreased or after allowing the cells to obtain ambient temperature.

RESULTS

Two sets of data (Figure1) indicate the resistance change across cell monolayers as a function of time to achieve steady state, *i.e.* that condition where resistance is consistent. Firstly, when cells were removed from an incubator at 37° to a biological safety cabinet at 22°C in medium with or without serum an initial decrease in resistance was recorded of around 20%. For a further 30 min. resistance was relatively steady and then climbed back to its original reading taking 70 min. In all, the time for steady state readings took 110 min. Secondly resistance changes were recorded after the cell medium had been changed at ambient temperature to medium either with or without serum. Little difference was observed as both sets of resistance fell initially by around 16% in 10 min. For a further 70 min. resistance remained unchanged and then climbed to its original value.

Resistance change as a function of temperature for cells in medium with or without serum shows an initial decrease of 13% and 17% respectively (Figure 2). An initial decrease was followed by a steady resistance from 31° to 26°C and then a rise to 22°C. A similar increase in resistance (average 22%) was recorded (Table 1) when cell monolayer resistance was measured in single wells moved from 37°C to 22°C.

When cells were either measured in one incubator or moved from one incubator to another before measurement (Table 2) the resistance change showed similar characteristics. This was a gradual fall for 25-30 min. and then a rise to original values within a total of 60 min. Cells in-situ showed a resistance fall of 16% and those that were moved between incubators one of 18%.

Variation in resistance recording was apparent when using the STX-2 electrode system (Table 3). In order to obtain a current between the outer and inner chambers, below and above the cell monolayer, one part of the electrode is placed in the outer separate chamber while the other shorter electrode is placed in the well insert. Depending on the position of the inner electrode, either in the center or at the edge of the well insert, different readings were recorded. At 37°C the average difference for six separate wells was 16% and at 22° 17%. As in previous experiments the change to a lower temperature elicits an initial decrease followed by an increase in resistance.

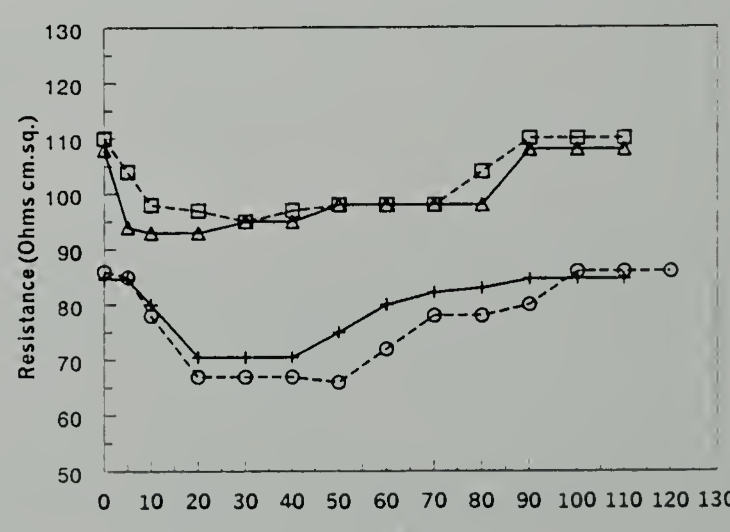

Figure 1. Resistance changes across cell monolayers as a function of time to achieve a steady state. Time to reach steady state from incubator at 37°C to safety cabinet at 22°C; — + — without added serum, — O — with added serum and time to reach steady state after a change of medium, — Δ — medium without serum, —□--- medium with serum.(n=3)

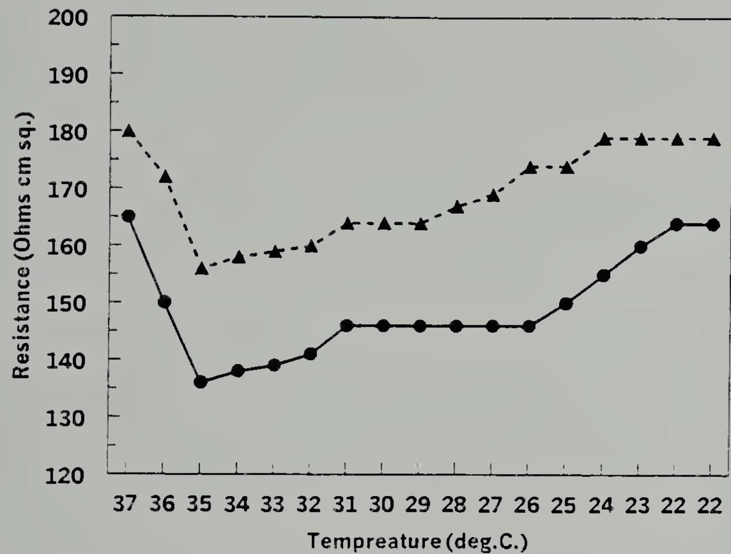

Figure 2. Resistance change across cell monolayers measured for each degree fall in temperature from 37°C to 22°C, — ● — serum free medium, --- ▲ --- medium with serum. (n+3)

Table 1: Absolute resistance values taken at 37°C and 22°C show an average increase of 22% when cells were moved from a higher to lower temperature. A "well" is a removable insert on which cells are grown as a monolayer on a permeable polycarbonate membrane. (n=3)

Well #	Ohms cm^2 (37°C)	Ohms cm^2 (22°C)	%
1	260 ± 1	340 ± 1	23
2	269 ± 1	335 ± 1	20
3	232 ± 1	340 ± 1	32
4	284 ± 1	340 ± 1	16
5	246 ± 1	335 ± 1	26
6	288 ± 1	335 ± 1	14

The voltometer was able to measure with a degree of accuracy of ± 1 Ohm.

Table 2: Absolute resistance over 1 hr of (a) cells measured in an incubator at 37°C and (b) after cells had been moved from one incubator to another at 37°C. (n=3) The percentage fall was 16% in 20 min. and 18% in 25 min. respectively after which the cells regained their original resistance readings.

Time (min)	Ohms cm^2 (a)	Ohms cm^2 (b)
0	220 ± 1	220 ± 1
5	216 ± 1	218± 1
10	195 ± 1	202 ± 1
15	183 ± 1	190 ± 1
20	183 ± 1	190 ± 1
25	188 ± 1	180 ± 1
30	192 ± 1	180 ± 1
35	197 ± 1	188 ± 1
40	210 ± 1	197 ± 1
45	212 ± 1	215 ± 1
50	220 ± 1	220 ± 1
55	220 ± 1	220 ± 1
60	220 ± 1	220 ± 1

The voltometer was able to measure with a degree of accuracy of ± 1 Ohm.

Table 3: Difference in absolute resistance measurements at two temperatures taken when STX-2 "chopstick" electrodes were held with one arm either at the edge or in the center of the well. Average percentage difference at 37°C is 16% and at 22°C is 17%. The electrodes were unable to record a steady resistance showing large variables of ± 10-20 Ohms cm^2. (n=3)

Well #	Ohm cm^2 (37°C)			Ohm cm^2 (22°C)		
	Edge	Center	%	Edge	Center	%
1	306	371	18	338	385	12
2	310	357	13	330	412	20
3	330	403	18	342	426	20
4	317	375	15	346	386	10
5	320	384	16	330	405	18
6	330	400	18	347	440	21

DISCUSSION

Any disturbance in the environment of cells grown as a single layer on transwell inserts of porous polycarbonate effects them in such a way as to transiently destabilize membrane potential. This is realized in an inconsistent resistance lasting in some cases for as long as 2 hr. Consideration therefore needs to be given to the accuracy of those resistance measurements either taken immediately after moving cell plates from the incubator or by a change of medium prior to addition of agents that alter resistance.

Cells of one layer are naturally delicate and pose problems of maintenance of correct pH, tonicity, temperature and nutrition. All of these lie within narrow boundaries depending on the type of cell. The mere mechanical action of physically handling cell plates containing such inserts appears to affect their stability. Of the variables proposed to account for this phenomena the simplest may be the movement of nutrition medium over the cell monolayer. Fluid disturbance creates a force that is transmitted to the apical surface of cells causing trauma, however minute, enough to alter resistance. Considering cells that form tight junctions when grown as monolayers take a considerable time (5-10 days) after confluence to do so indicates a cell specialty, which may be vulnerable to excess physical stress. The physical position of tight junctions formed proximal to the apical surface ensures their vulnerability to fluid movement.

Experiments were conducted in medium with or without fetal bovine serum to ascertain any difference. For instance if serum is present it may react with the Ag/AgCl electrodes by forming a proteinaceous layer, thereby giving false readings. This did not seem to be the case (Figure 1) as no significant difference is seen between the data.

Other than physical movement the major external factor influencing fluctuations in resistance appears to be temperature change. An average increase of 22% was recorded from individual wells (Table 1) confirmed by the observation of resistance change per degree but only after an initial decrease (Figure 2). When change of resistance was recorded closely per degree an initial decrease was apparent from 37° C to 35°of 17% for serum free medium and 13% for medium with serum. The graphs although starting at different absolute values show a similar pattern of gradual recovery to constant readings at 22°C.

Table 1 does not indicate an individual well decrease in resistance as seen in figure 2 because continuous readings were not observed. Cells were measured in the incubator and then moved to the safety cabinet to attain ambient temperature before measurements were taken. What occurs during that time is visible from figure1. Tight junctions are initially disturbed, indicated by a decrease in resistance after which they regain their "tightness" or integrity after around 90 min.

Since the structure function correlation of tight junctions as having both barrier and gate activity in partitioning between epithelium cells was discussed by Gumbiner, (1987) there have been profound advances in the molecular biology of these anastomosing intramembrane structures. Two major proteins, occludin and claudin, have been associated with the mechanism of tight junction strands and both are key components structurally and functionally. They are indirectly connected to zonal occludens (ZO) and it is the phosphorylation of occludin that initiates formation or deactivation of tight junctions. (Tsukite et al. 1996; Sakakibara et al.1997). Initially it was thought that occludin was the major functional component. However, further investigation led to the identification of claudin 1 & 2, integral membrane proteins that can form strand structures without occludin. (Furuse et al. 1998) The first of two extracellular loops formed by occludin contain an unusually high content of tyrosin and glysine residues (60%) (Tsukite and Furuse 1999). It was also observed

(Gumbiner 1987, Tsukita et al. 2001) that the number of tight junction strands correlate with TEER measurement and that these strands determine the barrier properties of tight junctions (Tsukita 2001). In addition to the extracellular loop of occludin it has been further proposed (Tsukita & Furuse 2000) that a membrane folding model of claudin –1 has two extracellular loops. That both occludin and claudin –1 exhibit extracellular loops and are therefore, in our cell model, exposed to the currents of nutrition medium leads to the speculation that this could initiate the mechanism of tight junction opening. If occludin is activated by fluid movement, this could give rise to a graduated influx of Ca^{2+} so activating tight junction strands. This in itself may be sufficient to partially activate ZO-1. TEER readings may decrease because of strand "loosening" and would require time after the removal of stress to regain original values.

Cells need time to recover after movement or change of medium in order to regain their junction tightness. Results suggest that tight junctions are not temperature sensitive between 37°C and 22°C as every alteration in measured resistance was accompanied by an immediate movement or disturbance. i.e. Change of location or addition of electrode (Table 2). At 37°C change in resistance is consistent with the magnitude of movement or disturbance. At the same temperature a pattern in change of resistance similar to movement from higher to lower temperature is recorded prompting the explanation that resistance change is independent of temperature.

Two other changes in environment need to be briefly considered, that of change of CO_2 tension when cells are moved from the incubator and the potential problem of air bubbles within the medium. Constant physical checks determined the absence of air bubbles but the lowering of CO_2 tension was not measured and remains a possible, although minor, cause of inconsistent resistance readings. A 5% CO_2 content is maintained within the incubator to ensure optimum pH, and when this is suddenly diminished it may affect cells by allowing the medium to become more alkaline. It is however, unlikely that this would have an immediate effect and is likely to be more prolonged. Similar results were recorded for the cell line HT29-Cl19A (unpublished) an adenocarcinoma clone of HT-29.

With respect to the measurement of cell resistance using the STX-2 "chopstick" electrode it was concluded that this method cannot be used accurately and is suitable only for estimated measurements. The differences in measurements from either the edge or the center of the well was considerable (Table 3). Given that the cells were equally spread and tight (confluent) the discrepancies may be due to slight bending or stretching of the electrodes when measuring from the well center. Although, measurements were also unsteady when taken from the edge, which could be partly due to the method of hand holding the electrodes in place.

The TEER method of measurement is generally accepted as reliable for the purpose of evaluating the open or closed state of tight junctions, the results of this present examination may be cautionary in emphasizing the necessity of allowing cells to reach a steady state before any applications or recordings are undertaken.

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THE ORIGIN OF SCIENCE

Gerard Elfstrom
Department of Philosophy
6080 Haley Center
Auburn University
Auburn, AL 36849-5210

Erwin Schrödinger was 61 years old in 1948. At that advanced stage of life, he had undertaken study of the major Greek thinkers. As a Nobel Laureate and one of the most distinguished physicists of the 20th century, he was blissfully free of the scrutiny of deans and promotion committees. Nonetheless, he was concerned that his recent avocation seem a mere diversion unrelated to his activity as a physicist. To counter this worry, he asserted that much could be learned about contemporary science by studying the work of ancient Greeks (Schrödinger, p. 3). Late in May he delivered a series of lectures at University College, London entitled, "Nature and The Greeks." He addressed the following theme:

> Remember the lines of Burnet's preface—that *science* is a Greek invention; that science has never existed except among peoples who came under Greek influence. Later in the same book he says, 'The founder of the Milesian School and therefore the first man of science [!] was Thales.' Gomperz says ... that our whole modern way of thinking is based on Greek thinking...(Schrödinger, p. 90).[1]

Schrödinger asserted that the Greeks had contributed several critically important elements to Western European science, but he believed that two stand above the rest because they define, as he says, "the peculiar, special traits of our scientific world-picture (Schrödinger, p. 90)." The first is, "The display of Nature can be understood (Schrödinger, p. 90)." The second, he believed, is less obvious but equally important, "The scientist subconsciously, almost inadvertently, simplifies his problem of understanding Nature by disregarding or cutting out of the picture to be constructed, himself, his own personality, the object of cognizance (Schrödinger, p. 92)."

Schrödinger was convinced that Thales, a citizen of the Greek colony Miletus, introduced these elements to Western civilization in the 6th century BC. For this reason he accepts Burnet's exuberant claim that Thales is the first man of science, the single individual who opened the way from the world of mythology to that of scientific investigation (though Schrödinger could not resist inserting an exclamation following Burnet's phrase).

These two elements, the conviction that nature can be understood and the useful maneuver of simplifying the scientist's task by ignoring human mental activity, are obviously critical to the development of Western European science, and they are part of its 'world-picture.' However, they are not the entire substance of Thales' achievement, and they don't capture essential features of scientific activity. Neither Thales nor the Greeks were the first to attempt to explain nature. Human mythology has the same goal.[2] The ancient myths provided explanations of nature's origin, structure, and natural phenomena, such as floods or storms, by describing them as the doings of the gods, the work of primordial human beings, or the activity of god-like animals. The presumption that nature can be understood is certainly a necessary condition for scientific endeavor, but it is not sufficient, since mythmakers had the same faith. Science relies upon a mode of explanation which differs markedly from that of mythology.

Thales, unlike the mythmakers, did not attempt to explain natural processes by reference to the activities of human-like agents. He did not allude to the doings of the gods or to magical transformations. This is also a clearly major step. However, Schrödinger's assertion that science removes the personality of the scientist from scientific scrutiny must be understood clearly. It appears that he believed simply that the scientist refrains from projecting human qualities onto the objects of study.[3] The Greeks are celebrated for 'inventing' nature, meaning that they first devised the conception of a natural realm which is distinct from that of humanity (Lloyd, pp. 417-34; Collingwood, pp. 29-31). This is clearly an important step, and it is as clear that Thales did refrain from projecting human qualities onto nature. If so, this second element is a close kin to the first, for the explanation the scientist offers of nature differs from that of the mythologists in not projecting human qualities onto nature, but, in addition, scientific explanation has other distinctive features, some of them introduced by Thales.

SCIENTIFIC EXPLANATION

To fully grasp the significance of Thales' contribution to the development of science, we must look closely at the kind of explanation of nature he offered and the context in which he derived it. Thales is famous, or perhaps infamous, for claiming that nature and everything in it is water. This does not seem a promising beginning for science. Aristotle, some 250 years after Thales' time, gives a clue to the significance of the assertion that all is water. In his *Metaphysics*, Aristotle observes:

> Of the first philosophers, most thought the principles which were of the nature of matter were the only principles of all things; that of which all things that are consist, and from which they first come to be, and into which they are finally resolved (the substance remaining, but changing in its modifications), this they say is the element and the principle of things, and therefore they think nothing is either generated or destroyed, since this sort of entity is always conserved, as we say... Thales, the founder of this school of philosophy, says the principle is water (Aristotle, pp. 1555-6, Vol. II).

The implication of this passage is that Aristotle believes Thales was addressing a clearly defined theoretical problem: Thales had observed that no extant thing springs from nothing at all. Rather, it emerges from some pre-existing material. He had also observed that things do not dissolve into nothingness when they cease to exist. Instead, they take on a different form. Nothing is erased completely. But, if this is so, how does it occur? Hence, Thales was wrestling with a problem, a theoretical problem which can be appreciated by scientists of the present time (Panchenko, pp. 391-4).[4]

Thales proposed that the question could be answered by presuming that there is one underlying material from which everything that comes into existence is created. He then asserted that water meets the requirements for this elemental substance. Aristotle speculates that he arrived at this conclusion as a result of noticing that water is intimately associated with life. Thales was inspired to make this connection, Aristotle believes:

> Perhaps from seeing that the nutriment of all things is moist, and that heat itself is generated from the moist and kept alive by it (and that from which they come to be is a principle of all things). He got his notion from this fact, and from the fact that the seeds of all things have a moist nature, and that water is the origin of the nature of moist things (Aristotle, p. 1556, Vol. II).

Aristotle's speculation is given weight by the fact that many of the ancient Greeks, quite possibly including Thales, believed that the world is an organism, a living thing (Collingwood, p. 31).[5] For those who believe that the world is an organism, rather than an inanimate being, it is entirely reasonable to believe water is its source, since, as Aristotle pointed out, water is closely associated with life.[6]

Aristotle is quick to note that the mythmakers also associated water with the origins of things, so it is entirely possible they influenced Thales' thinking. But, he then responds, "Thales at any rate is said to have declared himself thus about the first cause (Aristotle, p. 1556, Vol. II)."[7] So, even if Thales' inspiration came from mythology, Thales was the first to assert that water was the original source of all that exists and did so as a means of answering a significant problem—but, he did not weave a tale about the workings of the gods, as the mythmakers would have done. Thales' answer is the same as that of the mythmakers, but he did not employ it in the same way (Lloyd, pp. 286-7). He presented it as a theory devised to attempt to answer a scientific problem. Thomas Kuhn has insisted that the essence of scientific activity is problem solving (Kuhn, 1996, pp. 36-9). The problems that concern Kuhn, of course, are the scientist's problems of theoretical explanation. So, there are grounds for asserting that Thales engaged in one of the scientist's essential activities.

Thales' response to the problem of origins has an additional significant characteristic: It can be disputed, and it was (Panchenko, pp. 395-6; also see, Lloyd, pp. 115-6, 153-4). His train of successors also addressed the problem of origins, but they found weaknesses in Thales' response and provided answers of their own. These answers were rebutted in turn. Some of his successors claimed that air or some indeterminate stuff is the basic material of existence. Another of them, Democritus, gave a startlingly prescient answer: He claimed everything is composed of atoms, small, indivisible, material particles that differ from one another only in size and shape. Others, including Aristotle, asserted that there are several primordial substances. The critical thing is that each answer could be criticized, and successors could attempt to improve on it. Myths are simply passed from generation to generation. They may be modified along the way. However, they cannot be criticized nor can they be improved.

This chain of critical responses to, and attempted improvements on, Thales' answer, hints at what Thomas Kuhn believes is another crucial feature of scientific activity: It is conducted by a community of researchers who labor on a particular set of problems and share a number of crucial assumptions. Kuhn believes that it is possible for a solitary researcher to pursue scientific investigation, but he asserts that science does not begin until a community of researchers is formed that addresses a single set of problems and holds an array of assumptions in common (Kuhn, p. 13). If this is accepted, it is unimportant whether some unknown individual prior to Thales was the first to address a problem of science in scientific fashion. What matters is the indisputable fact that Thales initiated an arena of investigation that inspired the creation of a community of researchers. G.E.R. Lloyd illustrates the point nicely:

> Whether or not Anaximander developed some of his doctrines in reaction to those of Thales, and Anaximenes to those of Anaximander, with later philosophers we have texts in which they refer unmistakably to the theories of their predecessors, often mentioning them by name.... Although our information on the dates and places of residence of many writers is imprecise, we have enough evidence to be sure that at the end of the fifth century theorists working in widely separated parts of the Greek world were quite often acquainted with one another's doctrines in some detail. The ease with which ideas seem to have traveled, in a period when there were still formidable barriers to the passage of men and goods, is remarkable and deserves to be more fully investigated (Lloyd, pp. 115-6).

So, Thales' labors have several vitally important features of scientific activity: He addressed a clearly defined scientific problem, provided an answer which could be criticized and improved upon, and inspired the creation of a community of researchers. But, was he a scientist? The answer depends on our view of what a scientist is and what a scientist does. Our conception of what science is and what a scientist does has changed considerably over the centuries. One way to focus the question is to ask whether Thales engaged in the same array of activities as contemporary scientists. Simply and crudely, we can say that contemporary scientists do indeed address theoretical problems and seek to provide answers to them while avoiding reference to the doings of human-like agents or reliance on magical transformations. Their answers are routinely subjected to criticism and attempts at improvement, and, of course, scientists do function as part of a community of researchers. These qualities they share with Thales.

However, contemporary scientists also presume that any theories they develop must be subjected to empirical testing. This would never have occurred to Thales. He relied on reason and ordinary experience only. A common misperception is that none of the ancient Greeks relied on empirical testing. This is false (Lloyd, pp. 70-99 and 116-8). Some employed empirical studies, albeit sporadically, in anatomy, medicine, and astronomy (at least to the extent of seeking to conform their theories with empirical data). Nonetheless, the Greeks did not employ empirical verification in the routine and systematic fashion of the present age, and Thales, to the best of our knowledge, did not use it at all.

Furthermore, contemporary scientists commonly employ mathematics to probe the mysteries of nature. They presume that mathematics is an essential tool of investigation and analysis. Though Thales was a gifted mathematician who is believed to have devised several fundamental proofs of geometry, there is no record he thought to employ this instrument to assist his understanding of nature. This came later (Lloyd, p. 117-8). The first, and perhaps most exuberant, were the Pythagoreans, who were convinced that number is the foundation of all reality and that all reality could be explained in terms of number. A difficulty is that the Pythagoreans displayed a blithe disregard for empirical testing. They presumed that mathematical reasoning alone is the essential and adequate tool for grasping the essence of reality. A bit later, the astronomers, Ptolemy most notably, employed mathematics both to calculate the positions of heavenly bodies and also to test their theories. Astronomy, in fact, may have been the first discipline to embody all the elements of science, as contemporary practitioners would understand it (Lloyd, pp. 155-63).

In sum, Thales contributed several of the important elements of science, and he clearly initiated the chain of activity that has led to science as it is now practiced. In particular, he introduced theoretical problem solving, an essential feature of scientific activity. However, he was not a scientist in the current sense of the term, since he did not rely on empirical testing and he did not employ mathematics as a tool of scientific understanding. Rather, he planted a seed which eventually grew into science as it is presently understood. The other essential elements of science appeared surprisingly soon in Greek culture, but they were not employed in commonplace and organized fashion as they are at present.

WHY THERE? WHY THEN?

Clearly something extraordinary occurred in Miletus 2600 years ago that led the way out of myth and set in motion the process that led to scientific investigation. Unfortunately, we lack the detailed historical information what would yield a definitive answer to the questions of what occurred and why it did. Nonetheless, the scant information at hand allows the sketch of an answer—which must, nonetheless, remain speculative. Miletus was a bustling center of trade (Lloyd, p. 131). It was strategically located on the coast of what is now Turkey and commanded major trading routes of the day. People from differing cultures and differing religions intermingled in the course of commercial activity, but they also traded ideas and arguments (Schrödinger, pp. 55-6). It was not the sort of place where conflict of opinion could be settled by appeal to the authority of a religion or of a cultural tradition. The only common intellectual currency these disputing people of differing races, religions, and cultures would have enjoyed was that of bare reason.

Shielded by a chain of mountains from land invasion and pressure from inland empires, Miletus faced the Aegean Sea. Hence, while trade linked it to other civilizations, it was also politically independent. Though it was at the height of its prosperity in Thales' day, it was also politically unstable. Governments and governing arrangements came and went, and the merits of each were hotly debated by clusters of citizens, who thus became accustomed to voicing their opinions and were willing to defend them in public arenas (Lloyd, p. 131). Once again, reference to religion or customary practice would have had little influence on these knots of disputatious citizens.

Further, the leading citizens of Miletus, and Thales was among them, likely had the self-confidence commonly enjoyed by prosperous people who have gained their stature through their own efforts, their own wits, energies, and talents. They were likely not the sort of people who were accustomed to deferring to the authority of others and were not easily cowed by religious or governmental authority. Not incidentally, these prosperous and successful people enjoyed an essential requirement for intellectual activity, leisure. Aristotle argued that intellectual activity is the domain of leisured gentlemen, those able to seek understanding for its own sake undistracted by practical matters (Aristotle, Vol. II, pp. 1553-4; Lloyd, p. 131, 139). So, the science, mathematics, and philosophy of the era were practiced by small groups of individuals who sought these activities for the intrinsic satisfaction they brought. The Greeks were famously suspicious of the effort to seek practical application for their findings. Hence, the intellectual endeavors of the era were not overseen by religious authorities, nor were they supported and directed by governmental authority. They were undertaken on the free-wheeling initiative of private individuals, who were glad to ignore religious or practical concerns and follow their reasoning wherever it led.

This cluster of factors does not offer a direct causal mechanism for, but it does give a context in which one of the most remarkable features of Greek culture can be located. The

Greeks stood alone among the ancients in their fascination with theory (Lloyd, pp. 297-8). To each of the domains of intellectual activity they inherited or borrowed from older civilizations, they added the distinctive element of theoretical explanation. Geometry was first devised by the Egyptians, but they were content to employ it to serve practical ends only. The Greeks were the first to become fascinated with mathematics for its own sake, and they introduced the concept of mathematical proof (Bergamini, p. 39 and Lloyd, pp. 291-2). Thales, in fact, is thought to have invented the idea of a proof in geometry and is given credit for devising several critically important proofs (Bergamini, p. 41; Panchenko, pp. 404-5). Astronomy had long been practiced in Babylonia, but the Babylonians simply gathered observations and calculated the positions of heavenly bodies. Only the Greeks added theories of why celestial bodies moved as they did (Lloyd, pp. 293-5). Medicine is likely as old as humanity. Once again, though, other cultures and older peoples were interested only in successful cures. The Greeks alone were moved to contrive theories of the origins of illness and the secrets of good health (Lloyd, pp. 295-8). Something in their culture moved Greeks to seek out theoretical explanations. Thales may have been the single individual who introduced this proclivity, or he may simply have caught a passion which was already present in the culture. We may never know which is correct. Sadly, we have no idea of what may have driven the ancient Greeks to a fascination with theory. It is, nonetheless, clear that they had it and that they exercised it in several domains. Hence, they, possibly in the person of Thales, contributed the essential element of theoretical explanation to science.

Further, the Greeks were famously proud and competitive. The small circles of inquirers provided individuals opportunity to gain that which they desired greatly, fame and status (Panchenko, pp. 405, 412-4). An individual who offered a particularly elegant proof of geometry or who concocted a beguiling theory of the movement of the heavenly bodies received the considerable reward of instant and enthusiastic acclaim. Nonetheless, status was neither easily won nor easily retained. The Greeks were a notoriously impertinent lot. They routinely laced their discussions with ridicule—even when examining the ideas of illustrious forebears (Lloyd, p. 115). Bold theoreticians could expect their ideas to be carefully scrutinized, and they would also expect that others would work to come up with something better. So, they understood that their assertions had to be carefully supported and clearly stated. Though science, then as now, was valued for its intrinsic merit, science, then as now, offers the significant incentives of fame and prestige to adept practitioners. These are powerful motivators, and Greeks of the classical era were as avid to win them, as are contemporary scientists. Nonetheless, adulation was always mixed with irreverence. The Greeks were never wary of criticizing illustrious elders, and could count on adulation for themselves if they could uncover flaws in the thinking of celebrated thinkers.

No one can presently say how love of argument, enjoyment of lively conversation with small knots of peers, and the universal desire for recognition, leavened by irreverence, came together in Miletus to produce individuals who were eager to construct theories which could be employed to address scientific problems. The scraps of information on life in Miletus offer the basis for plausible speculation, but that is all. What is certain is that life in Miletus and its citizen Thales initiated a thread of scientific investigation which leads directly from the 6th century BC to the present age of scientific inquiry. So, Schrödinger's basic insight is correct: We can learn a great deal about science by examining its Greek origins.[8] He is also correct to believe that the Greeks developed the concept of nature which Western European cultures continue to employ. However, he overlooks the crucial element that Thales added to scientific explanation, that of theoretical explanation devised to address a scientific problem.

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[1] Were he writing today, Burnet would likely make these points in more nuanced fashion. It is true that Islamic science drew from the Greeks and in turn nurtured the revival of scientific activity in Medieval Europe. However, both India and China had science and had it at about the same time as the Greeks. It is true, though, that these scientific traditions languished eventually. It is reasonable to say that the international culture of science of the present day is closely shaped by that of Western Europe, and it is also true that this science traces its roots back to Thales. In addition, given our scant information on early Miletus, it is entirely possible that someone other than Thales was the first to formulate a scientific problem and answer it in reasoned fashion. As will be seen shortly, however, it is clear that he did initiate a chain of investigation that leads eventually to Western European science.

[2] Schrödinger implicitly recognizes this in his text, for he mentions the activity of the mythologists, but he then points out that Thales' explanations did not rely on the doings of gods or on magic. So, the key element of science is not simply explanation, but explanation of a particular sort.

[3] For example, Schrödinger says at one point, "This momentous step—cutting out oneself, stepping back into the position of observer who has nothing to do with the whole performance... (Schrödinger, p. 93)."

[4] Inferences about the thinking of someone who lived 2600 years ago and left no written work should be made with caution. Aristotle lived 250 years after Thales, and is therefore in better position to understand his thinking than we. But, 250 years is still a long time. Furthermore, as Lloyd (p. 128) notes, Aristotle was interpreting Thales' activity through the lens of his own concerns. Nonetheless, considerable weight is given to these inferences by the fact that the train of Thales' successors clearly were dealing with this problem and criticized or endorsed his own position in terms of the requirements of this problem.

[5] Schrödinger construes Aristotle to assert that Thales believed everything is alive (Schrödinger, p. 65). Aristotle's texts, however, are less forthright. There are only two passages in Aristotle that touch on this topic. In *On the Soul*, Aristotle says, "Certain thinkers say that soul is intermingled in the whole universe, and it is perhaps for that reason that Thales came to the opinion that all things are full of gods (Aristotle, p. 655, Vol. I)." Earlier in the same work, Aristotle says, "Thales, too, to judge from what is

recorded about him seems to have held soul to be a motive force, since he said that the magnet has a soul in it because it moves the iron (Aristotle, pp. 645-6, Vol. I)." In neither of these passages does Aristotle commit himself flatly to the view that Thales believed every extant thing is alive.

[6] Contemporary investigators also find this notion reasonable. They argue that the presence of liquid water is an essential condition for life (Chyba and Phillips, pp. 47-9 and Fry, pp. 242-54). Hence, researchers looking for signs of extraterrestrial life seek evidence of the presence of liquid water. Of course, they don't share Thales' assumption that everything therefore *is* water.

[7] Alert readers will likely have already noticed a lacuna in this argument: To assert that water is the source of life is not the same as asserting that living beings are composed of water or are modifications of water. And, of course, it is not obvious that simply one type of stuff underlies all existence. Thales' successors soon addressed these matters, however.

[8] Thomas Kuhn echoes Schrödinger's claim a few years later. He begins *The Structure of Scientific Revolutions* by arguing that failure to appreciate its history has led scientists to misunderstand the nature of science (Kuhn, 1996, pp. 1-9). Much of Kuhn's thinking is inspired by the Scientific Revolution of Galileo and Newton. However, in a presentation made in 1980, Kuhn reveals that the seminal insight that led to his thinking about scientific revolution was inspired by his frustrated study of Greek science. He calls it his "Aristotle moment." In 1947 he was a graduate student at Harvard preparing a lecture on Aristotle's *Physics* for an undergraduate course in physics for nonscientists. At first, he was puzzled and irritated by what he found. Aristotle seemed to make no sense at all. After a period of frustrated mulling, he had a flash of insight. His insight was that Aristotle was a physicist all right, but a very different physicist than Newton. Aristotle asked different questions than Newton and employed different concepts. Once Kuhn recognized this difference, he found Aristotle's analyses to be most astute. Kuhn claims that this experience initiated the chain of events which ultimately resulted in *The Structure of Scientific Revolutions* (Kuhn, 2000, pp. 15-20).

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GYMNOSPERMS OF NORTHEAST ALABAMA AND ADJACENT HIGHLANDS

Daniel D. Spaulding
Anniston Museum of Natural History
Anniston, AL 36202

J. Mark Ballard
Jordan, Jones, & Goulding, Inc.
Tucker, GA 30084

R. David Whetstone
Jacksonville State University
Jacksonville, AL 36265

Illustrated by:
Marion Montgomery
Anniston Museum of Natural History
Anniston, AL 36202

INTRODUCTION

This paper is a guide to all the cone-bearing plants (conifers) of the northeast Alabama. Plant species occurring in adjacent highland counties are also part of this flora. The study area includes 13 specific and infraspecific taxa, representing a total of 7 genera, 3 families, 2 orders, 2 classes, and 2 divisions. This guide includes illustrations, maps, identification keys, habitats, distributional data, conservation status, uses, and pertinent synonymy.

The flora is based upon herbarium specimens deposited at the Jacksonville State University Herbarium (JSU) and other southeastern herbaria which include Vanderbilt University (VDB), University of Alabama (UNA), University of North Alabama (UNAF), and Auburn University (AUA). Data from appropriate literature are also included. Nomenclature primarily follows Flora of North America [FNA] (1993+) and more recent publications.

The area delineated as Northeast Alabama includes Blount, Calhoun, Cherokee, Clay, Cleburne, Cullman, DeKalb, Etowah, Jackson, Jefferson, Limestone, Madison, Marshall, Morgan, Randolph, Saint Clair, Shelby, and Talladega counties (Figure 1). Adjacent highland counties include Bibb, Chambers, Chilton, Coosa, Lauderdale, Lawrence, Tallapoosa, Tuscaloosa, Walker, and Winston. The highlands of Alabama consists of the following Provinces: Interior Low Plateau (Highland Rim), Appalachian Plateau (Cumberland Plateau), Ridge and Valley, and Piedmont Plateau (Figure 2).

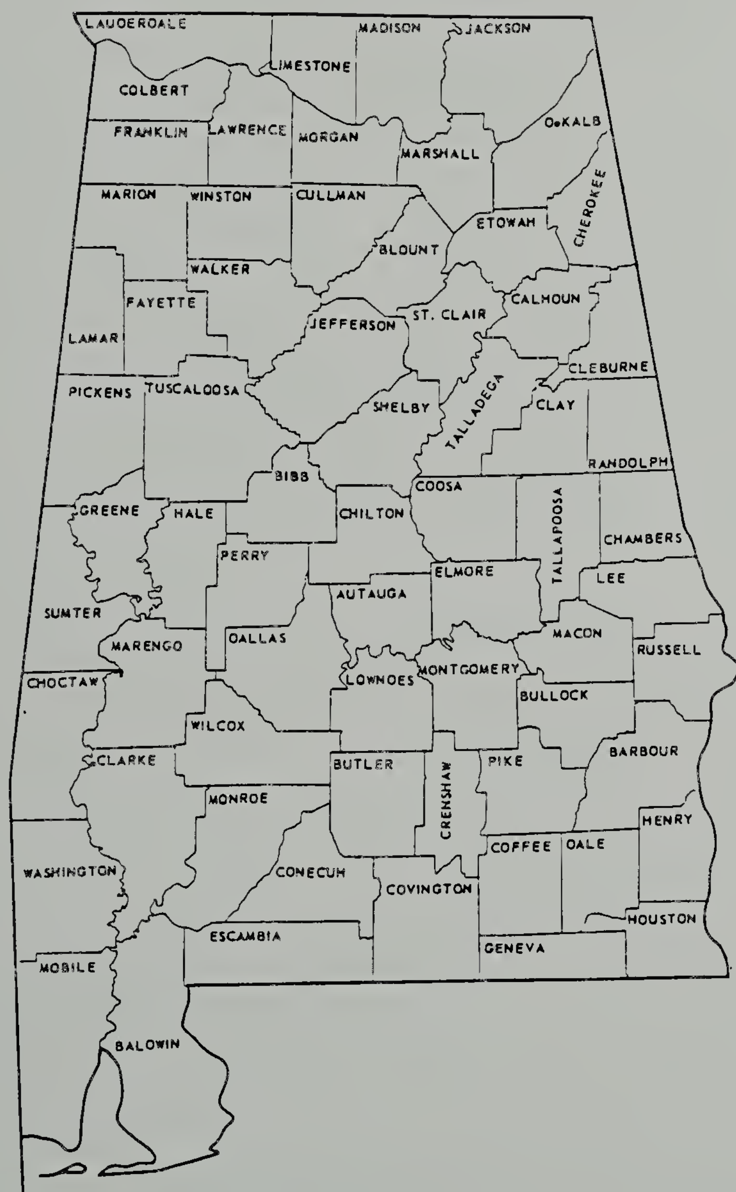

Figure 1. County Map of Alabama

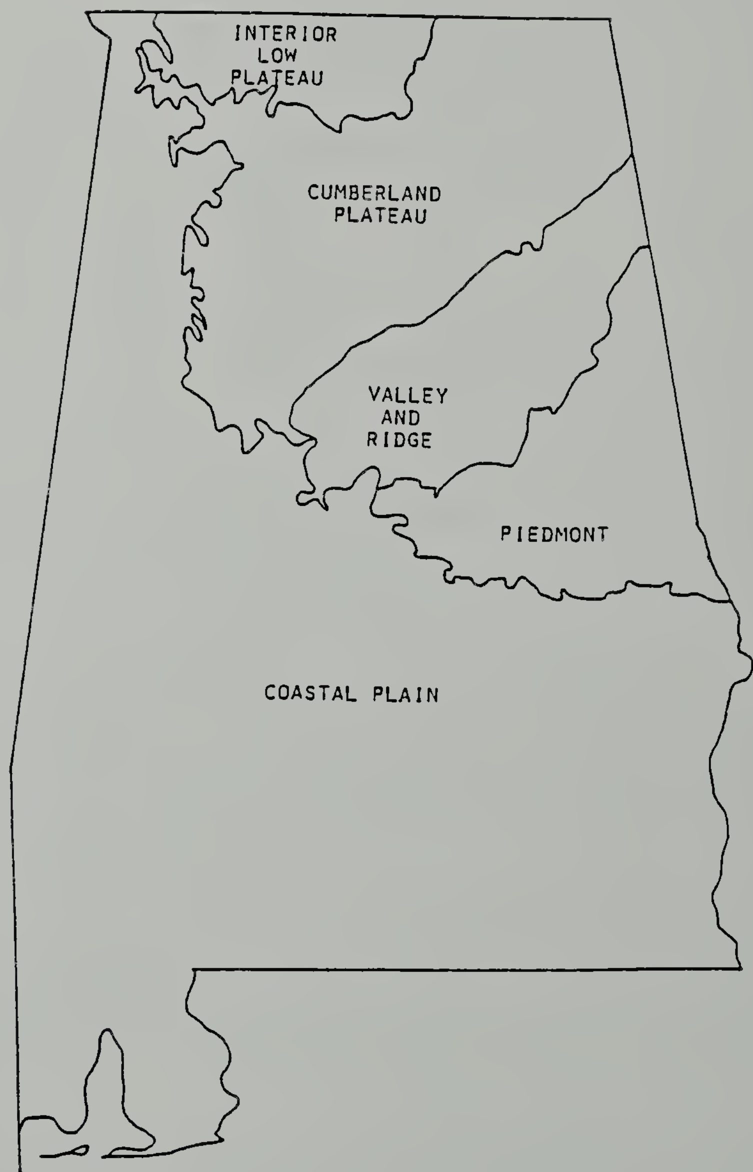

Figure 2. Physiographic map of Alabama

FORMAT

Families, genera, specific and infraspecific taxa are arranged alphabetically within major vascular plant groups (divisions, classes, and orders). Information on specific and infraspecific taxa is set up in the following format: **Number.** *Name* author(s) [derivation of specific and infraspecific epithets]. VERNACULAR NAME. Habit; nativity (if exotic). Pollen and seed shedding dates. Habitat data; highland provinces; relative abundance; [occurrence on Coastal Plain]. Conservation status. Wetland indicator status. Comments. *Synonyms.*

Introduced taxa are followed by a dagger ( ). Species of conservation concern are followed by a star (★). The coded state ranks (ANHP 1994, 1996, 1997, 1999) are defined in Table 1. Wetland indicator status codes (Reed 1988) are defined in Table 2. Relative abundance is for occurrence in the study area and not for the whole state. Frequency of occurrence is defined as follows, ranging in descending order: *common* (occurring in abundance throughout), *frequent* (occurring throughout but not abundant), *occasional* (known in more than 50% of the region but in scattered localities), *infrequent* (known in less than 50% of the region in scattered localities or occurring in restricted habitats), *rare* (known from only a few counties and restricted to specific localities), and *very rare* (known from only a single or few populations; mostly narrow endemics, disjuncts, and peripheral taxa). Synonyms are from Mohr (1901)- M; Small (1933)- S; Radford *et al.* (1968)- R; and Clark (1971)- C. Suggested pronunciation, author(s), date of citation, common name, and derivations are provided after each genus.

Distribution maps are typically for 18 counties in the northeast region of Alabama. The maps are expanded to adjacent highland counties for taxa that are rare or peripheral. Key to symbols are as follows: Filled circle (●) = documented at Jacksonville State University herbarium; filled square (■) = documented at another herbarium; open circle (o) = reported in literature.

Table 1. Definition of state ranks.

Code	Definition
S1	*Critically imperiled* in Alabama because of extreme rarity or because of some factor(s) making it especially vulnerable to extirpation from Alabama.
S2	*Imperiled* in Alabama because of rarity or because of some factor(s) making it very vulnerable to extirpation from the state.
S3	*Rare or uncommon* in Alabama.
S4	*Apparently secure* in Alabama, with many occurrences.
S5	*Demonstrably secure* in Alabama and essentially "ineradicable" under present conditions.
SH	*Of historical occurrence*, perhaps not verified in the past 20 years, and suspected to be still extant.
SR	*Reported*, but without persuasive documentation which would provide a basis for either accepting or rejecting the report.
SU	*Possibly in peril* in Alabama, but status uncertain.
S?	*Not ranked* to date.

Table 2. Definition of wetland indicator codes.

Code	Status	Probability of Occurrence
OBL	Obligate Wetland Species	Occurs with estimated 99% probability in wetlands.
FACW	Facultative Wetland Species	Estimated 67%-99% probability of occurrence in wetlands, 1%-33% probability in nonwetlands.
FAC	Facultative Species	Equally likely to occur in wetlands and nonwetlands(34%-66% probability).
FACU	Facultative Upland Species	Estimated 67%-99% probability of occurrence in nonwetlands, 1%-33% probability in wetlands.
UPL	Obligate Upland Species	Occurs with estimated 99% probability in uplands.
NI	No Indicator Status	Insufficient information available to determine an indicator status.

Note: Positive or negative signs indicate a frequency toward higher (+) or lower (-) frequency of occurrence within a category.

KEY TO GYMNOSPERM FAMILIES

1. Leaves fan-shaped and deciduous; venation dichotomous (forking)........................Ginkgoaceae
1. Leaves needle-like or scale-like, evergreen or deciduous; venation not dichotomous.
   2. Deciduous trees; bark fibrous; seed cones round and woody with scales that do not overlap (valvate); leaves alternate.. Cupressaceae (*Taxodium*)
   2. Evergreen trees or shrubs; bark not fibrous; seed cones round to oblong and woody (with overlapping scales) or fleshy (with scales that do not overlap); leaf arrangement various.
      3. Leaves needle-like; leaf arrangement alternate or in fascicles (bundles); seed cones woody and large (more than 3 cm long) with overlapping (imbricate) scales ....Pinaceae
      3. Leaves scale-like or needle-like; leaf arrangement opposite or whorled, not in fascicles; seed cones fleshy and small (up to 1 cm long)......................Cupressaceae (*Juniperus*)

DIVISION I. GINKGOPHYTA
Class 1. Ginkgoöpsida
Order 1. Ginkgoales

1. GINKGOACEAE (Maidenhair Tree Family)

Selected reference: Whetstone, R. D. 1993. Ginkgoaceae. In: Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico. 3+ vols. New York and Oxford. Vol. 2, pp. 350-351.

1. GINKGO {GINK-go} Linnaeus 1771 • Maidenhair Tree • [Chinese *yin*, silver, and *hing*, apricot, in reference to the appearance of the seed which has an outer fleshy coat and a hard silver-colored inner coat.]

1. *Ginkgo biloba* Linnaeus [two lobed]. MAIDENHAIR TREE; GINKGO. Figure 1. Deciduous tree; native to China. Pollen shed March - April; seeds shed August - November. Ginkgo is widely planted as an ornamental, but not documented to escape from cultivation in Alabama. The unusual shape of the crown, natural resistance to disease, and yellow leaf color in the fall make this a favorite street and park tree. Female (ovulate) trees produce an abundance of seeds, which develop a particularly obnoxious odor; the planting of ovulate ginkgos is often discouraged for this reason. Seeds (canned with fleshy outer coat removed) are sold in ethnic markets as "silver almonds" or "white nuts." Oils from the outer coat are known to cause dermatitis in some humans. Ginkgo is a popular medicinal herb. An extract from the "nuts" are used to calm upset people as well as treat a variety of other ailments (Krochmal 1984). The species is doubtfully naturalized in North America despite about two centuries of cultivation here. Most, if not all, ginkgoes exist only in cultivation. It is identical to ancient fossils and is sometimes called a "living fossil." The name "maiden-hair" alludes to the shape of the leaves which resemble leaflets of the Maiden-hair Fern (*Adiantum*).

DIVISION II. PINOPHYTA (=Coniferophyta)
Class 1. Pinopsida (=Coniferopsida)
Order 1. Pinales (=Coniferales)

1. CUPRESSACEAE (Redwood or Cypress Family)

Selected reference: Watson, F. D. and Eckenwalder, J. T. 1993. Cupressaceae. In: Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico. 3+ vols. New York and Oxford. Vol. 2, pp. 399-401.

1. Evergreen trees or shrubs; leaves opposite or in whorls; female (seed) cones berry- or drupe-like, to 9 mm long; plant of upland habitats .... *Juniperus*
1. Deciduous trees; leaves alternate; female cones dry, hard, typically greater than 20 mm long; plant of wetlands .... *Taxodium*

Note: A small population of *Cupressus arizonica* Greene, Arizona Cypress, is established along a fencerow in Calhoun County. This native of the western United States, was probably seeded in by birds. No other populations are currently known within the study area. Though superficially similiar to *Juniperus virginiana*, this cypress is easily separated by its large (2+ cm) woody cones in comparison to the smaller (6 to 10 mm) berry-like cones of *Juniperus virginiana*. In addition, a specimen of *Platycladus orientalis* (Linnaeus) Franco [*Thuja orientalis* Linnaeus], Oriental Arborvitae, has been collected in Jackson

County. Because Arizona Cypress and Oriental Arborvitae are rare escapes and unlikely to become established within the study area, they have not been included within this treatment.

1. JUNIPERUS {jew-NIP-er-us; yoo-NIP-er-us} Linnaeus 1753 • Juniper; Red-Cedar • [*Juniperus*, Latin name for Juniper.]

Selected reference: Adams, R. P. 1993. *Juniperus*. In: Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico. 3+ vols. New York and Oxford. Vol. 2, 412-420.

1. Prostrate to spreading shrub; all leaves linear "often awl-like", margins upturned, 5 to 15 mm long, glaucous line on upper surface; seed cones (berries) axillary... *J. communis* var. *depressa*
1. Upright tree; mature leaves scale-like, 2-5 mm long, margins not upturned and lacking glaucous line on upper surface, often forming overlapping pairs; young or stump sprout leaves needle-like, 5-10 mm long, in whorls of three; seed cones (berries) terminal .... *J. virginiana*

1. *Juniperus communis* ★ Linnaeus [in clumps] var. ***depressa*** Pursh [flattened]. GROUND JUNIPER; COMMON JUNIPER. Figure 2. Evergreen shrub. Pollen shed March - April; female cones maturing in. second or third year. Rocky ledges and slopes; Ridge and Valley (Chocolocco Mountain); very rare. State Rank, S1. Wetland Indicator Status, UPL. The "berries" have been used medicinally to increase urination, induce menstration, and relieve gas. Indians used the needles and twigs to make a poultice for wounds (Krochmal 1984). Large doses are considered toxic, causing kidney failure and digestive irritation (Foster and Duke 1990). The "berries" are also used to flavor gin. Synonym: *Juniperus sibirica* Burgsdorff - S.

2. *Juniperus virginiana* Linnaeus [Virginian]. EASTERN RED-CEDAR. Figure 3. Evergreen tree. Pollen shed January - March; seeds shed September - November of first year. Dry sites, including slopes, roadsides, fencerows, and open disturbed areas; infrequently occurs within "drier" floodplain areas; all highland provinces; common; [Coastal Plain]. Wetland Indicator Status, FACU-. The aromatic and lustrous wood of this tree has been long prized for furniture production. During the early 1900s, this species was the sole source for pencil wood. When all merchantable timber had been harvested, lumbermen began to tear down eastern red-cedar rail fences and barns to meet the demands of the pencil trade (Peattie 1991). Southern Red-cedar, *Juniperus virginiana* Linnaeus var. *silicicola* (Small) E. Murray, is very similiar to this species. The distribution of southern red-cedar is limited to the Gulf and Atlantic Coastal Plain of the southeastern states. The two varieties can be distinguished by the following characteristics. *Juniperus virginiana*: female cones 4-6 mm; male cones 3-4 mm; scale-like leaves acute at apex; crown spire shaped to rounded. *Junipers virginiana* var. *silicola*: female cones 3-4 mm; male cones 4-6 mm; scale-like leaves obtuse to acute at apex; flattened crown. Synonym: *Sabina virginiana* (Linnaeus) Antoine - S.

2. TAXODIUM {tax-OH-dee-um} Richard 1810 • Bald-Cypress • [*Taxus*, generic name of yew, and Greek *-oides*, like.] Following Watson and Eckenwalder (1993), this genus (along with the family Taxodiaceae) is included within Cupressaceae. Other treatments, such as Radford *et al.* (1968) and Clark (1971), recognized Taxodiaceae (the Redwood Family).

Selected reference: Watson, F. D. 1993. *Taxodium*. In: Flora of North America Editorial

Committee, eds. 1993+. Flora of North America North of Mexico. 3+ vols. New York and Oxford. Vol. 2, pp. 403-404.

1. Branches with leaves mostly in 2 ranks (specimens should not be from juvenile individuals, fertile branchlets, stump sprouts, terminal vegetative branchlets, or late-season growth); leaves mostly spreading; leaves narrowly linear, 5-17 mm long .... *T. distichum* var. *distichum*
1. Branches with leaves not in 2 ranks; majority of leaves ascending (and often overlapping) in a vertical plane along twigs; leaves narrowly lanceolate, 3-10 mm long .... *T. distichum* var. *imbricarium*

1. *Taxodium distichum* (Linnaeus) Richard var. ***distichum*** [two-ranked]. BALD-CYPRESS. Figure 4. Deciduous tree. Pollen shed March - April; seeds shed September - October. Edge of reservoirs and rivers, backwater sloughs, and low wet areas adjacent to railroad rights-of-way; Cumberland Plateau, Ridge and Valley; infrequent; [chiefly Coastal Plain]. Wetland Indicator Status, OBL. Bald Cypress is planted in yards and in reservoirs and other impoundments for wildlife habitat. This species usually does not escape in urban environments, but becomes readily naturalized in wetland systems. Only those populations believed to be native or naturalized were included within this treatment.

2. *Taxodium distichum* (Linnaeus) Richard var. ***imbricarium*** (Nuttall) Croom [over-lapping]. POND-CYPRESS. Figure 5. Deciduous tree. Pollen shed March - April; seeds shed September - October. Banks and shallow waters of reservoirs along the Coosa River; Ridge and Valley; very rare; [chiefly Coastal Plain]. Wetland Indicator Status, OBL. Because of the its well-known durability, both varieties of *Taxodium distichum* are highly prized for their lumber. Bald-Cypress is more characteristic of flowing water swamps, whereas Pond-Cypress is more often found in still-water swamps. Synonym: *Taxodium ascendens* Brongniart - S, R.

2. PINACEAE (Pine Family)

Selected references: Price, R. A. 1989. The genera of Pinaceae in the southeastern United States. J. Arnold Arbor. 70: 247-305. Thieret, J. W. 1993. Pinaceae. In: Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico. 3+ vols. New York and Oxford. Vol. 2, pp. 352-354.

1. Leaves round or diamond-like in cross section and in fascicles (bundles); seed cones more than 2 cm long .... *Pinus*
1. Leaves flat in cross-section, not fascicled; seed cones less than 2 cm long .... *Tsuga*

1. PINUS {PYE-nus} Linnaeus 1753 • Pines • [Classical Latin name for pine.]

Selected reference: Kral, R. 1993. *Pinus*. In: Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico. 3+ vols. New York and Oxford. Vol. 2, pp. 373-398.

1. Leaves "needles" in bundles of 5; mid-branches of mature trees whorled; cones narrow and elongate; cone scales without prickles. .... *P. strobus*
1. Leaves in bundles of 2 or 3; mid-branches of mature trees not whorled; cones not narrow and

elongate; cone scales with prickles.

2. Leaves usually 3 per fascicle; leaf more than 14 cm long.
   3. Leaves more than 25 cm long; leaf sheaths (around base of fascicle) more than 2 cm long; terminal buds silvery white; mature seed (female) cones usually more than 15 cm long .... *P. palustris*
   3. Leaves less than 25 cm long; leaf sheaths less than 2 cm long; terminal buds brownish; mature seed cones usually less than 15 cm long *P. taeda*
2. Leaves usually 2 per fascicle; leaf less than 14 cm long.
   4. Leaves twisted and less than 6 cm long; twigs bark smooth .... *P. virginiana*
   4. Leaves straight to slightly twisted and more than 6 cm long; twigs bark rough .... *P. echinata*

1. *Pinus echinata* Miller [spiny]. SHORTLEAF PINE; SOUTHERN YELLOW PINE. Figure 6. Evergreen tree. Pollen shed March - April; seeds shed September - October. Upland woods; all highland provinces; common; [Coastal Plain]. Wetland Indicator Status, UPL. A valuable lumber tree with a high fuel value. The inner bark and young male cones of pines can be used as an emergency food in times of need. These parts have a disagreeable taste, but are nutritious (Peterson 1977).

2. *Pinus palustris* Miller [marshy]. LONGLEAF PINE; YELLOW PINE. Figure 7. Evergreen tree. Pollen shed March - April; seeds shed September - October. In our area, usually on slopes and ridges with sandy soil; Cumberland Plateau, Ridge and Valley, Piedmont Plateau; infrequent; [Coastal Plain]. Wetland Indicator Status, FACU+. One of the few pines to exhibit a grass-like stage which helps to protect it from fire. Periodic fires clear away ground litter and allow seeds a better chance to germinate. Because this species is not as easily machine planted, sites that are clear-cut are often replanted in Slash or Loblolly pines to maximize pulpwood rotations (Brown and Kirkman 1990). Trees are tapped for their turpentine and resin. Heartwood splinters (which have lots of resin) are often called "light-wood" or "fat-wood" in the south and are used to start fires. Wood is strong and durable. Turpentine oil has been used to treat colic, diarrhea, tapeworms, and constipation (Krochmal 1984). Northeast Alabama is one of the few areas with montane long-leaf pine communities that supports colonies of Red-cockaded Woodpeckers.

3. *Pinus strobus* Linnaeus [cone]. EASTERN WHITE PINE. Evergreen tree. Figure 8. Pollen shed March - April; seeds shed August - September. One collection has been made in the Cumberland Plateau, in Dekalb County, and may have been introduced. It is also reported for Lawrence County in the Bankhead National Forest. Wetland Indicator Status, FACU. This pine is extensively planted in the northern part of the state. White Pine is found mainly in the Blue Ridge of Georgia and Tennessee and throughout the more northern states in the eastern United States and Canada. An important timber tree with soft and light wood that is often used for cabinets, paneling, and interior trim. Once prized as a wood for the masts of ships in colonial times. Young shoots, stripped of their needles, were once made into a candy by New Englanders (Fernald and Kinsey 1958).

4. *Pinus taeda* Linnaeus [ancient name for resinous pines]. LOBLOLLY PINE; OLD-FIELD PINE. Figure 9. Evergreen tree. Pollen shed March - April; seeds shed October - November. Low woods, upland woods, roadsides and fields; all highland provinces; common; [Coastal Plain]. Wetland Indicator Status, FAC. A "loblolly" is a natural depression where this tree sometimes grows (Little 1980). One of the most important lumber trees in the South. This species is often attacked and killed by the Southern Pine Beetle (*Dendroctonus frontalis*). Slash Pine, *Pinus elliottii* Engelmann, is native to the southern coastal plain and is similar to Loblolly, but can be identified by its glossy leaves that are in bundles of 2 and 3. Tar from this tree has been used in a vapor that is inhaled to treat pulmonary diseases. It is also applied as a salve for skin diseases (Krochmal 1984). Seeds of pines are eaten by game birds such as turkey and quail; songbirds such as Red Crossbill, Evening Grosbeak, Brown-headed Nuthatch, Pine Siskin, Carolina Chickadee, and Pine Warbler; and mammals such squirrels and mice (Martin, *et al.* 1951).

5. *Pinus virginiana* Miller [Virginian]. SCRUB PINE; VIRGINIA PINE. Figure 10. Evergreen tree. Pollen shed March - May; seeds shed September - November. Dry, rocky soils in woods and woodland borders, especially on slopes and ridges; Cumberland Plateau, Ridge and Valley, Piedmont Plateau; common. Wetland Indicator Status, UPL. Wood is weak, but is used for pulp and sometimes railroad ties. Also cultivated as a Christmas tree. Spruce Pine, *Pinus glabra* Walter, resembles Scrub Pine, but has leaves more than 6 cm long and grows in low woods on the Coastal Plain.

2. TSUGA {tsu-GAH} (Endlicher) Carrière 1855 • Hemlocks • [Japanese name for the native hemlock of Japan.]

Selected reference: Taylor, R. J. 1993. *Tsuga*. In: Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico. 3+ vols. New York and Oxford. Vol. 2, pp. 362-365.

1. *Tsuga canadensis* (Linnaeus) Carrière [of Canada]. EASTERN HEMLOCK; CANADA HEMLOCK. Figure 11. Evergreen tree. Pollen shed March - April; seeds shed September - November. Cool, moist slopes and ravines; Cumberland Plateau; rare. Wetland Indicator Status, FACU. The soft, brittle wood is sometimes utilized for pulp and crating, but is rarely used for lumber. This tree makes poor firewood because it pops and sends off sparks. Bark was used by pioneers as a source of tannin. Trees would often be stripped of their bark and left to die (Brown and Kirkman 1990). Young needles can be used to make a pleasant tasting tea that contains Vitamin C (Peterson 1977). Widely planted in the northern part of the state as an ornamental tree. Naturally growing in Pisgah Gorge in Jackson County and in the Bankhead National Forest in northwest Alabama. An old record from 1949 exists for Jefferson County. This specimen was collected in rocky soil about 20 feet above Village Creek approximately 2 mile north of Lindberg. A collection of hemlock made in Dekalb County might have been introduced.

ACKNOWLEDGMENTS

We are grateful to Robert Kral, the "botanical king" of the Southeast, for his thorough review of this flora. His many comments and suggestions greatly improved this work. We also appreciate the late Warren Herb Wagner, Jr. and Jack Short for reading through the manuscript and providing valuable insight. Finally, we thank Verna Gates for her grammatical review of this document.

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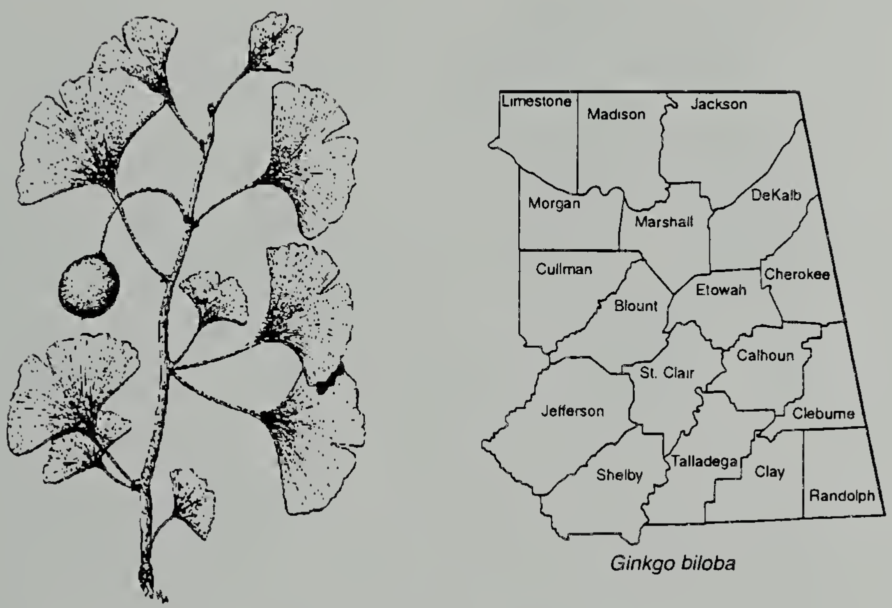

Figure 1. *Ginkgo biloba*- Maidenhair Tree

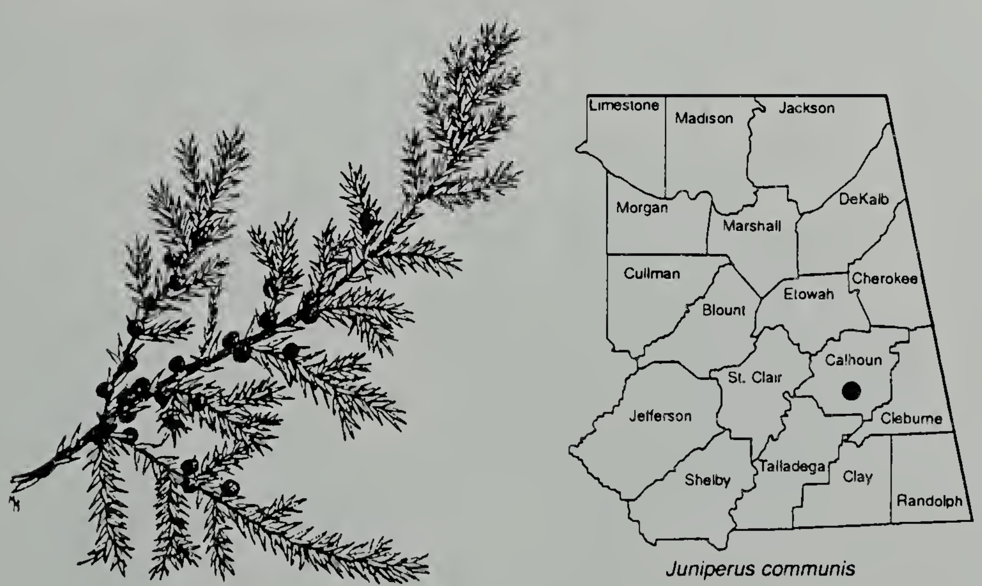

Figure 2. *Juniperus communis*- Ground Juniper

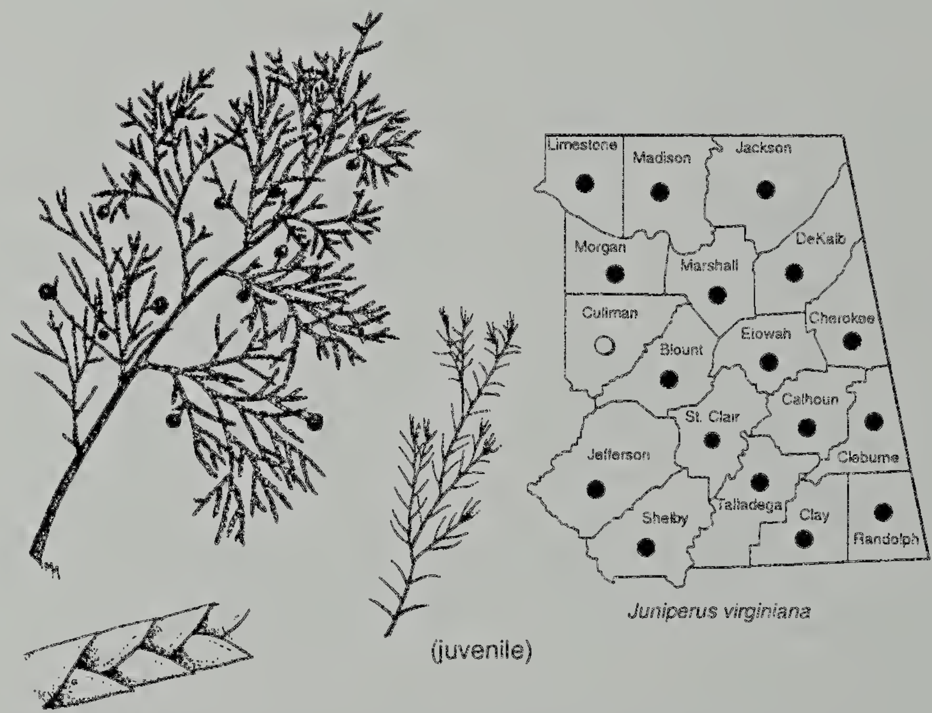

Figure 3. *Juniperus virginiana*- Eastern Red-Cedar

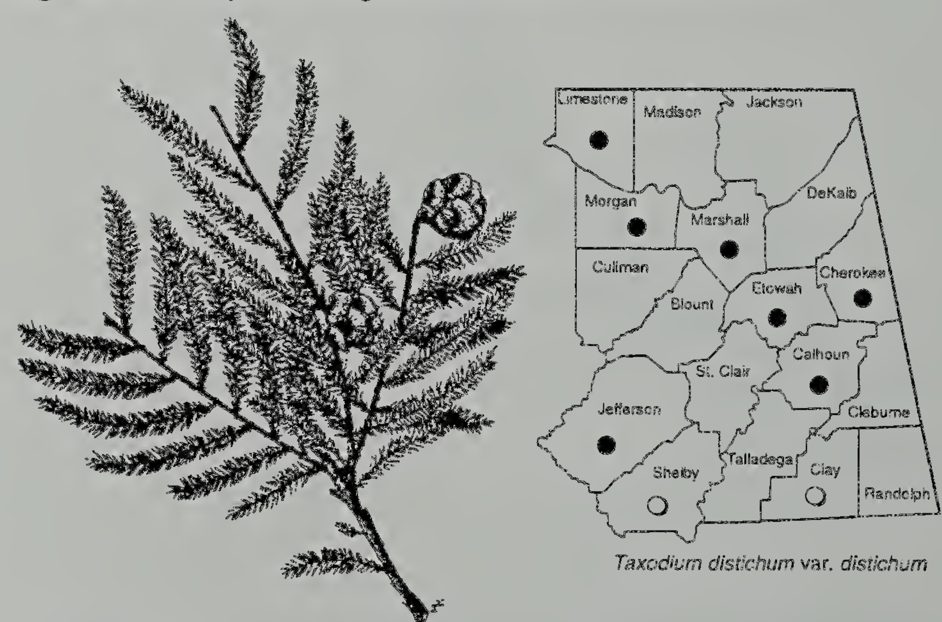

Figure 4. *Taxodium distichum* var. *distichum*- Bald-Cypress

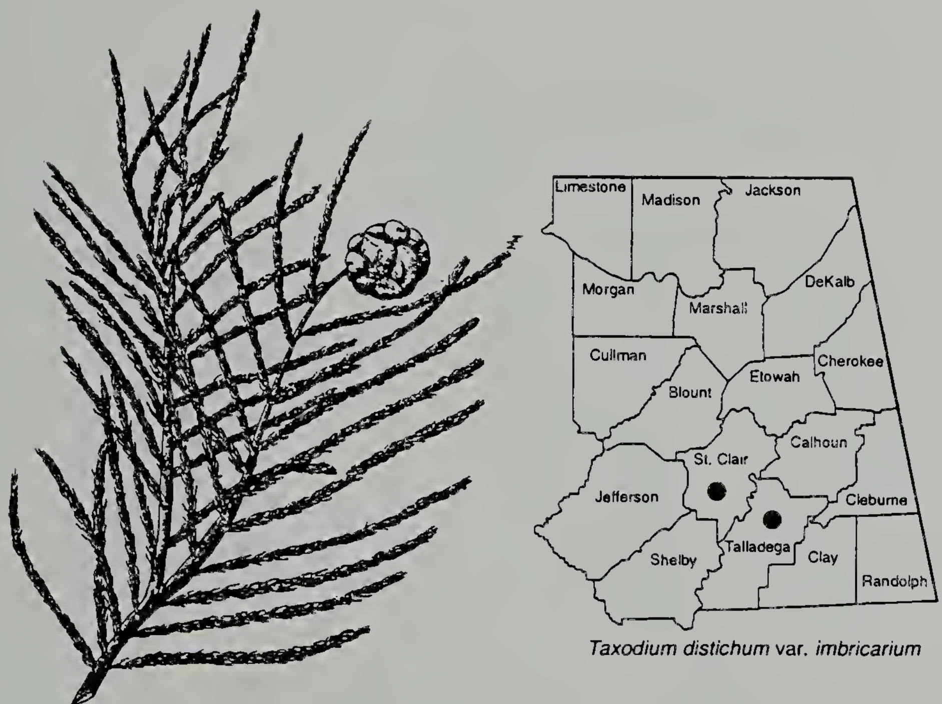

Figure 5. *Taxodium distichum* var. *imbricarium*- Pond Cypress

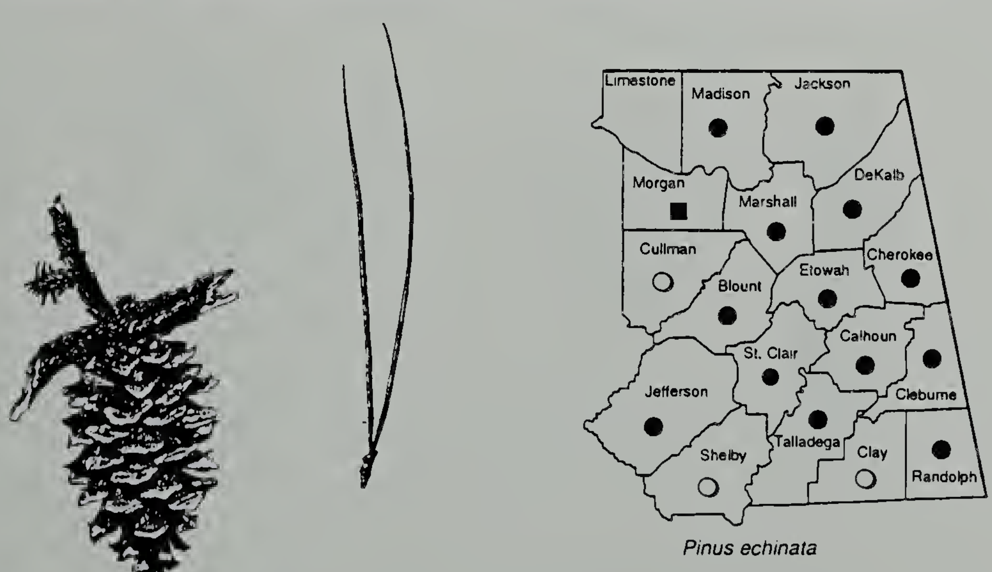

Figure 6. *Pinus echinata*- Shortleaf Pine

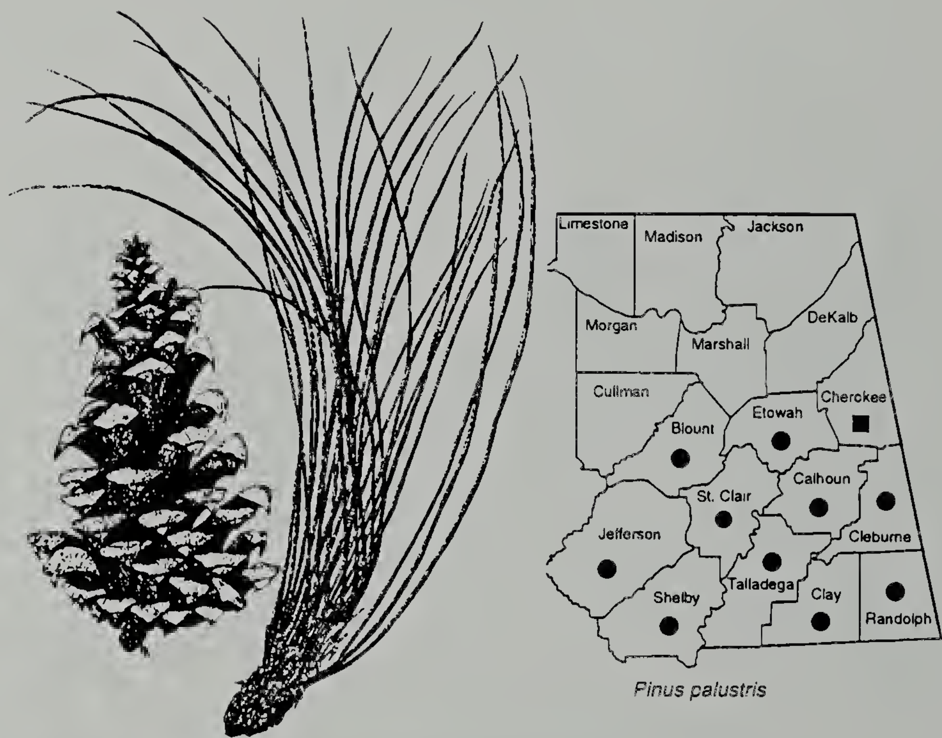

Figure 7. *Pinus palustris*- Longleaf Pine

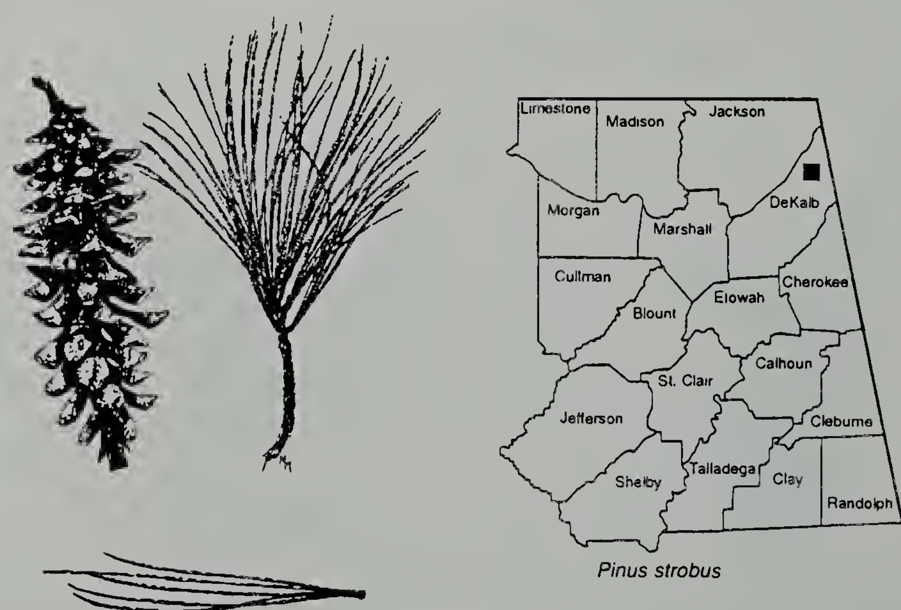

Figure 8. *Pinus strobus*- White Pine

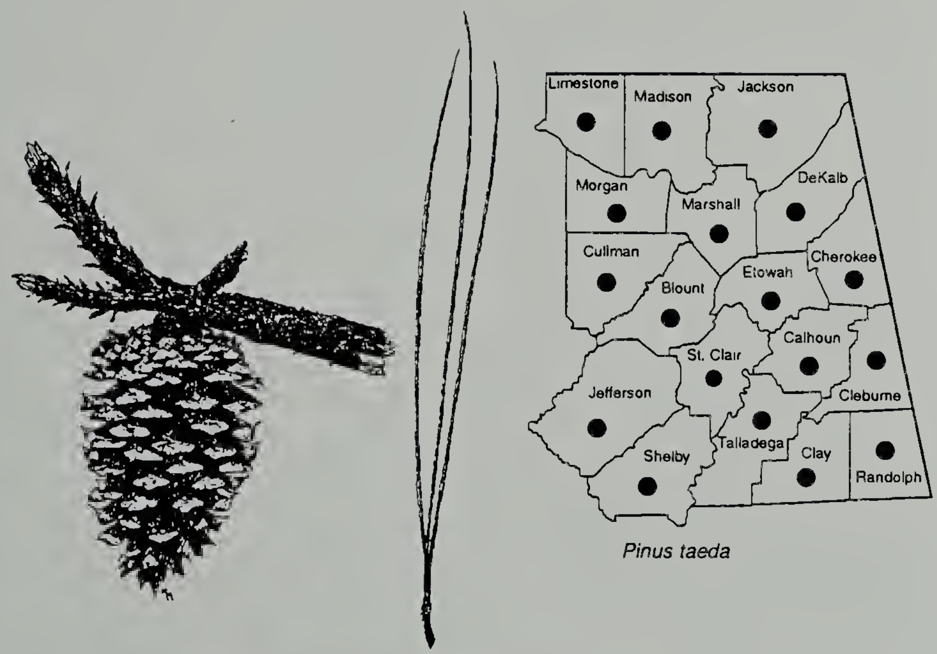

Figure 9. *Pinus taeda*- Loblolly Pine

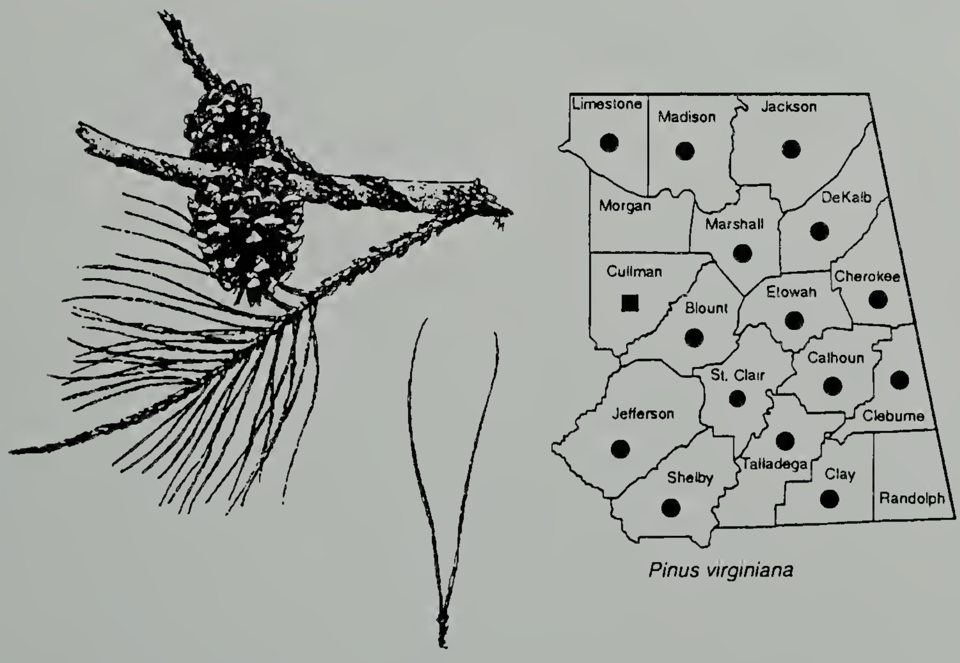

Figure 10. *Pinus virginiana*- Scrub Pine

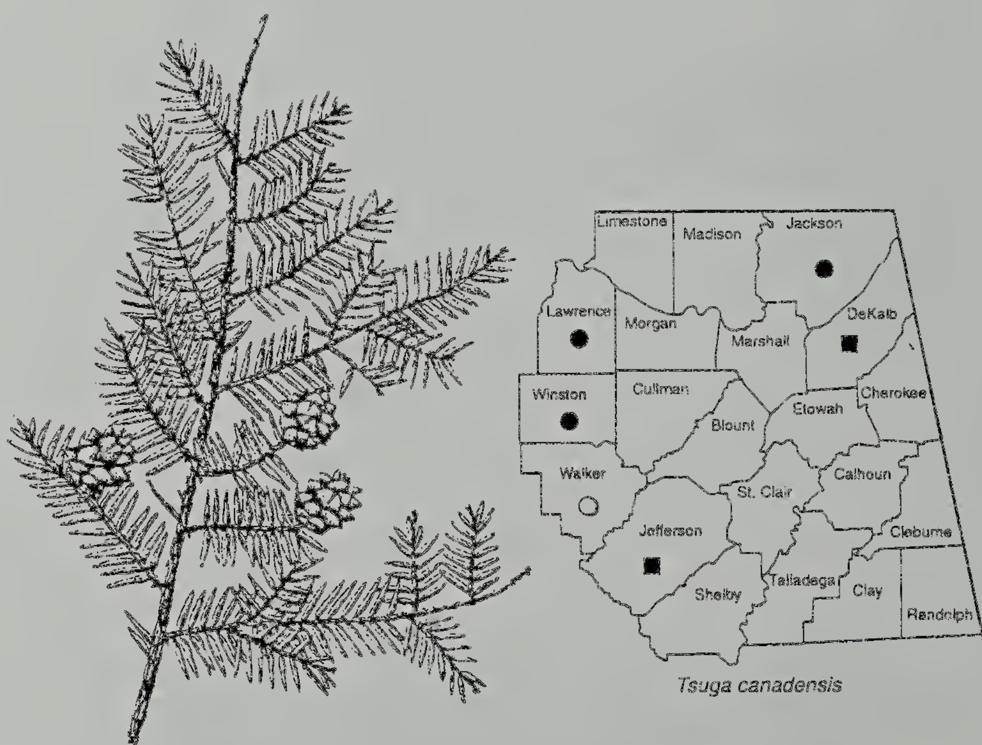

Figure 11. *Tsuga canadensis*- Eastern Hemlock

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BOOK REVIEW

SECULAR STANCHIONS OF CIVILIZED EXISTENCE CAN SAVE THE PLANET

James T. Bradley
Department of Biological Sciences
Auburn University
Auburn, AL 36849
bradljt@auburn.edu

The Future of Life, Edward O. Wilson, 229 pp. Alfred A. Knopf, New York, 2002.

Harvard University Professor Edward O. Wilson is likely the best known, most widely respected, and also the most controversial biologist of the present and last century. Recognizing that the impact of his contributions extend far beyond the realm of biology, many, myself included, view him as one of the most important thinkers of the twentieth century. He has taught biology at Harvard University for over 40 years and published his research on social insects for as many decades. E.O. Wilson is the author of two Pulitzer Prize-winning books, *On Human Nature* (1978) and *The Ants* (1990), the founder of the discipline of sociobiology, and a relentlessly brave and articulate public educator, spokesperson, and political activist for the conservation and preservation of biodiversity. His most recent book, *The Future of Life*, is a highly significant work on the latter subject. It documents humankind's reckless and ignorant fouling of its nest, yet offers realistic hope that a solution for a twelfth hour salvation of the biosphere is still within our grasp.

The book begins with a personal letter from Edward (O. Wilson) to Henry (David Thoreau) written while Wilson sits near the little house that Henry built at the edge of Walden Pond in 1845. "You left us too soon, and your restless spirit haunts us still," Wilson writes. Then he explains to Henry that his purpose in visiting Waldon Pond is "to become more a Thoreauvian, and with that perspective better to explain to you, and in reality to others and not least to myself, what has happened to the world we both have loved." Wilson's letter to Thoreau encapsulates each of the points and ideas that become amply documented and developed in the succeeding chapters of the book.

In the letter Wilson reflects that soon after Henry's too early exit from this world in 1862, wood-powered America approached its first energy crisis which was relieved by coal. In concert with the Industrial Revolution, the world's population rapidly burgeoned to its present six plus billion people, the majority of whom are extraordinarily poor. The frontier West in now largely used to grow agricultural plants to feed cattle, pigs, and poultry. Half of the tropical rain forests have been cleared, and species of plants and animals are going extinct at a rate one hundred times faster than before the advent of *Homo sapiens*. Half of the extant species of living things are projected to be extinct within 100 years. Wilson sums up our present situation: "We are in a bottleneck of overpopulation and wasteful consumption." That is the bad news. But Wilson does not leave his friend, and us, hopeless.

The letter continues with a piece of good news. Population growth has slowed and will probably peak by the end of the 21st century at 8-10 billion people. Also, some experts calculate that there is enough arable land to maintain this many people at a decent standard of living, while at the same time preserving the most vulnerable animal and plant species. Wilson argues that the modern, technoscientific culture that is destroying the biosphere can, and must, also be the source of its salvation. Inside our present bottleneck of breeding and consumption rages a race between destructive and potentially beneficent technoscientific forces. For humanity to emerge from the bottleneck in better shape than when it entered, science and technology must be guided by a global land ethic. Wilson describes the land ethic he has in mind as "one based on the best understanding of ourselves and the world around us that science and technology can provide."

Wilson's description is a nice addendum to Aldo Leopold's seminal definition of a Land ethic published over half a century ago in *A Sand County Almanac And Sketches Here and There*: "A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise." After the letter to Henry, the first half of the book is devoted to describing the problem. The second half gives cause for optimism and proposes a solution.

Documentation of Earth's environmental crisis includes discussions of tropical rain forest biology and deforestation, demographics of population, wealth, and consumption (supporting an average American's life style requires 24 acres of land annually while a citizen in a developing nation is supported by just 2.5 acres), ecological effects of global warming, and long term effects of unintended and intentional introduction of exotic plants and animals into different regions of the world. In discussing the rate extinction of species worldwide, Wilson notes that beginning with the emergence of agriculture about 10,000 years ago, humanity has played the role of planetary killer, "concerned only with its own short-term survival." I was surprised to read that the longer an area has been colonized by agriculturists, the slower is the rate of present extinctions. But the explanation, although alarming, makes perfect sense. The most vulnerable species, which are many, are the first to go; after a while, the rate of extinction declines as the more robust species begin being picked off. Thus a slow rate of extinction in a long developed region may mean that entire ecosystems have already disappeared. Numbers, statistics, and examples abound in this section of the book. My response was shocked incredulity, despair, guilt, and anger. Then came Wilson's reasons for optimism.

In the penultimate chapter titled "For the Love of Life" we read about biophilia, the innate tendency of humans to focus upon and affiliate emotionally with living things. "Biophilia" was first introduced and fully developed by Wilson in his 1984 book with the same name (Harvard Univ. Press, Cambridge, MA). This "sense of genetic unity, kinship, and deep history...that bond us to the environment" is a source of emotional energy within ourselves to be tapped for reasoned action aimed at preserving (and restoring where possible) what remains of the planet's diversity.

Reasoned progress toward global, environmental conservation depends "on cooperation among three secular stanchions of civilized existence: government, the private sector, and science and technology." Wilson looks to democratic governments to provide ethically based laws and regulatory practices that give long-term benefits to the governed. One such benefit is a healthy biosphere. The private sector, working within the constraints established by government, is the economic engine of society. If vigorous, this engine can turn the turbines of science and technology which Wilson sees as supplying the knowledge that government and people need in order to make informed choices. Imagining this kind of cooperation may sound like "pie-in-the-sky" thinking at first, but Wilson proceeds to describe an important facilitating link-pin that is already quite well developed; namely, Nongovernmental Organizations (NGCs) presently spearheading the global conservation effort. Between 1956 and 1996, the number of NGOs committed to humanitarian and/or environmental causes increased from 985 to over 20,000. These are headed by the U.S. based World Wildlife Fund and The Nature Conservancy, each with memberships exceeding one million. NGOs can fund establishment of environmental reserves throughout the world without the political adversities that would need to be overcome in order for national governments to do the same. Once reserves are established and even enlarged, they are still terribly vulnerable to encroachment by "human activity and invasion by alien organisms." What are needed to stabilize the reserves are natural corridors connecting them across continents. There are NGOs actively working right now for the establishment of such corridors, and Wilson writes that a realistic vision for one set of natural corridors in the Western Hemisphere would result in a continuous swath of natural lands stretching from Alaska to Bolivia. Ultimately, education, informed voting within working democracies, and NGOs' examples could win entire governments over to the cause.

Wilson also sees room for religion to play an important role in this otherwise secular endeavor. He notes that stewardship of the earth and a responsible environmental ethic are compatible with the present day theology of all three Abrahamic religions: Islam, Judaism, and Christianity. Although science and religion see many things differently, Wilson maintains that there is no apparent reason why they cannot cooperate productively in the arena of global environmental conservation.

The Future of Life is a major contribution toward helping to build a working coalition among the three secular stanchions Wilson has named. It provides facts, and it details realistic courses of action that could slow and even reverse humanity's destructive behavior. One must look hard to find reason to criticize this book. For me, the only disappointing aspect of the entire text was the lack of credit given to Wisconsin conservationist, Aldo Leopold, for originating the "land ethic" concept in his 1949 essay by that title. Wilson gives us facts and specific courses of action. Leopold inspires us with prose akin to poetry:

"...the individual is a member of a community of interdependent parts. His instincts prompt him to compete for his place in the community, but his ethics prompt him also to co-operate."

"Abraham knew exactly what the land was for: it was to drip milk and honey into Abraham's mouth. At the present moment, the assurance with which we regard this assumption is inverse to the degree of our education."

"Obligations have no meaning without conscience, and the problem we face is the extension of the social conscience from people to land."

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