CONTENTS

ARTICLES:

Eastern Hemlock Decline and Persistence of Disjunct Populations Near Its Southern Boundary
Justin L. Hart ......................................................... 174

Twentieth Century Climate Change in Alabama
Jonathan M. Herbert .................................................... 181

Abundance, Identification, and Prospective Participation of Bacteria on Gopher Tortoise Shell Degradation
Valerie M. Johnson, Craig Guyer, Matthew D. Shawkey, and Sharon R. Robert ................................. 190

Pteridophytes of Southeast Alabama: Dichotomous Keys, Illustrations and Distribution Maps
Michael Woods and Alvin R. Diamond, Jr. ........................................ 200

BOOK REVIEW:

Human Perfection Through Biotechnology: Should We Go For It?
Drew Humphries and James T. Bradley ........................................... 238

AUTHORS INDEX: ................................................................. 243
EASTERN HEMLOCKDECLINE AND PERSISTENCE OF DISJUNCT POPULATIONS NEAR ITS SOUTHERN BOUNDARY

Justin L. Hart
Department of Geography, University of North Alabama
Florence, Alabama 35632
Correspondence: jhart13@gmail.com

ABSTRACT

Eastern hemlock (Tsuga canadensis) is a long-lived, shade tolerant tree species that sometimes occurs in pure stands on lower slopes and stream valleys of Appalachian forests in eastern North America. The range of eastern hemlock extends from southern Quebec and Ontario southward to Georgia and along the Cumberland Plateau to Alabama. Eastern hemlock is currently being threatened by the hemlock woolly adelgid (Adelges tsugae), a defoliating insect. The decline of eastern hemlock is consistent with the contagion hypothesis of range collapse, and disjunct eastern hemlock populations near the southern boundary of the species may not be extirpated because of their geographic isolation.

INTRODUCTION

Geographic ranges of organisms are dynamic, and range features (e.g. size and shape) are the results of organism characteristics and complex interactions with the surrounding environment both past and present (Brown et al., 1996; Channell and Lomolino, 2000a). The abundant-center distribution is a longstanding theory in biogeography. The theory is based on the assumption that a species’ range should contain more favorable habitat near the center where populations should be larger and less variable (Sagarin and Gaines, 2002). Habitat quality is assumed to decrease with increasing distance from the core where populations should become more fragmented (Brown, 1984; Channell and Lomolino, 2000b). The demographic hypothesis of range collapse is based on the abundant-center distribution theory and assumes when extinction forces arise, a species’ range should implode and the last populations should persist near the core of the historic distribution. The demographic hypothesis also assumes that population size influences extinction, which is not always true. A number of plant and animal species (e.g. American chestnut (Castanea dentata (Marsh.) Borkh.) and California condor (Gymnogyps californianus Shaw)) now exist only at the periphery of their former ranges because of the spatial dynamics of the particular extinction force rather than population density.

Extinction factors often move across the landscape like a contagion. When such movement occurs, the last location impacted should be the most isolated from the initial location of the extinction force, regardless of the point of origin (Lomolino and Channell, 1995, 1998; Channell and Lomolino, 2000b). Extinction factors that move in such a manner are generally transferred through anthropogenic activities such as the introduction of alien pests (Lomolino and Channell, 1995). Eastern hemlock (Tsuga canadensis (L.) Carr.) is currently facing an extinction force in the hemlock woolly adelgid (Adelges tsugae Annand; HWA) and may become another species restricted largely to the periphery of its current range. The decline of eastern hemlock attributed to HWA is unique because the spatial dynamics of extirpation can be observed and documented as they occur.

Eastern hemlock decline within the core of the species’ range has been widely documented by independent studies (e.g. Orwig et al., 2002; Ellison et al., 2005; Lovett et al., 2006). However, dispersal of the HWA to disjunct eastern hemlock populations has not been discussed. This void in the literature may be the result of the complex nature of range collapse dynamics that are difficult to empirically test. Here, using field observation, eastern hemlock and HWA literature, and current biogeographic theory, I present the hypothesis that eastern hemlock populations removed from the contiguous range of the species may not become infested. I focus on disjunct eastern hemlock populations near the southern range boundary of the species.

Figure 1. Range of eastern hemlock and the hemlock woolly adelgid in eastern North America (from Little 1971 and U.S.D.A. 2006).
**EASTERN HEMLOCK AND THE HEMLOCK WOOLLY ADELGID**

Eastern hemlock is a long-lived, shade tolerant species that sometimes occurs in almost pure stands on lower slopes and stream valleys of Appalachian forests in eastern North America. Eastern hemlock modifies microclimatic and pedologic characteristics of inhabited sites and is considered a keystone species (Orwig et al., 2002; Ellison et al., 2005). The range of eastern hemlock extends from southern Quebec and Ontario southward to Georgia and along the Cumberland Plateau to Alabama (Fig. 1). Disjunct populations are present in southern Michigan, western Ohio, southern Indiana, Kentucky, Tennessee, Alabama, Georgia and east of the Appalachian Mountains. Characteristics of many disjunct populations have been documented, including those in southern Indiana (Friesner and Potzger, 1944), Alabama (Segars et al., 1951; Harper, 1952; Hart and Shankman, 2005), Georgia (Bormann and Platt, 1958) and North Carolina (Oosting and Hess, 1956).

Currently, eastern hemlock is threatened by the defoliating HWA. The HWA is a small, aphid-like insect native to Japan that was first documented in eastern North America near Richmond, Virginia in the 1950s (Souto et al., 1996). The HWA has spread from the central Appalachian Mountains and now occurs in the northern and southern range of eastern hemlock (Fig. 1). The adelgid feeds on ray parenchyma of newly developed twigs, causing needle loss and eventually tree mortality (Young et al., 1995). The HWA has infested and killed eastern hemlock in all size and age classes. It has been hypothesized that eastern hemlock could functionally disappear from eastern forests over the next several decades because the species does not generally re-establish after mortality caused by the HWA and is being replaced throughout its range by mixed hardwoods and sometimes Rhododendron species in the south (Ellison et al., 2005). The loss of eastern hemlock is predicted to have long-term impacts on ecosystem structure and function (Lovett et al., 2006). The adelgids are parthenogenetic and reproduce rapidly (twice annually) (McCline, 1989a). They are mainly transported by wind, but also by birds and mammals, including humans (McCline, 1989b, 1990). The HWA is currently dispersing in a diffuse pattern through the contiguous range of eastern hemlock at ca. 30 km year⁻¹. The dispersal and impacts of the HWA through the contiguous range of eastern hemlock illustrate the contagion hypothesis defined by Lomolino and Channell (1995) and Channell and Lomolino (2000a, 2000b).

In the northern section of its range, eastern hemlock typically occurs in almost pure stands with sparse understories. In the southern section of its range, eastern hemlock typically occurs in mixed stands in riparian zones and in moist protected coves (Ellison et al., 2005; Shankman and Hart, 2007). Although in the southern portion of its range eastern hemlock is not ubiquitous across the landscape but is largely confined to riparian areas, populations are not widely scattered and are linked by valleys created by the well-developed stream networks of the unglaciated Appalachian Highlands.

In specific locations, the advancement of the HWA through the northern range of eastern hemlock has been slowed by cold temperatures. Winter temperatures below -30 °C have led to high mortality of HWA, but populations have quickly recovered and HWA may eventually develop resistance to cold as northward migration continues (Parker et al., 1998, 1999). In general, HWA dispersal has proceeded unimpeded. The HWA is also advancing through the southern range of eastern hemlock. Near its southern range boundary, eastern hemlock occurs in isolated populations disjunct from the contiguous range. These populations are confined to deeply incised stream valleys and are more widely scattered across the landscape relative to populations within the contiguous boundary. Disjunctions at its southern extent have been shown to be reproductively viable and stable populations that provide the same ecosystem functions as elsewhere in its range (Hart and Shankman, 2005).

**SOUTHERN RANGE OF EASTERN HEMLOCK**

Once the HWA reaches the southern boundary of the contiguous range of eastern hemlock, diffuse dispersal will cease because the HWA is host specific to Tsuga. In many cases, long distances separate disjunct eastern hemlock populations from the contiguous range. For the adelgid to infest outlying populations at eastern hemlock’s southern boundary in Tennessee, Alabama, and Georgia, it must colonize new sites via jump dispersal over long distances. For example, disjunct populations at the southernmost boundary of eastern hemlock in Alabama are separated from the contiguous range by ca. 300 km. Also, gaps exist in the presence of disjunct populations near its southern boundary as eastern hemlock is largely absent from north-central Alabama for reasons that have yet to be explained. The spatial pattern of eastern hemlock occurrence near its southern boundary will not foster jump dispersal or “island hopping” of the HWA from one population to another until the southernmost extent is reached. The unfavorable habitat (i.e. lack of eastern hemlock) between the contiguous range and the disjuncts at the boundary may require the HWA to follow the sweeps mode of dispersal (i.e. long distance dispersal with low probability of success) to reach the full southern range of its host.

The HWA is a sessile insect which spends most of its life attached to its host plant. However, there are a few days between egg hatch and the initiation of feeding when nymphs actively move about their host. The nymphs are light in weight and can be carried by wind over great distances (McCline, 1989a). Because the nymphs are agile (i.e. passively distributed), their dispersal is dependent upon wind speed and direction at the time of their activity, which is generally in the spring. Many disjunct populations of eastern hemlock occur to the south and west of the species’ contiguous range. The dominant winds in the southeastern United States are westerlies and would not favor the transport of HWA to the disjunct populations to the south or west. Rare, severe wind events such as those associated with tornadoes or extreme low pressure systems have the potential to transport HWA over great distances. In the southeastern United States, tornadoes are common with the majority occurring in March and April. However, these storms generally follow directional paths to the northeast (Suckling and Ashley, 2006). Thus, most tornadoes in the region move from the periphery towards the contiguous range of eastern hemlock, and would likely not facilitate the long-distance dispersal of HWA to outlying populations.
Not only are disjunct eastern hemlock populations separated from the contiguous range by long distances, but they are also quite small. Some of these populations consist of less than 30 total individuals with as few as five trees that occupy positions in the forest canopy (Hart and Shankman, 2005). Only a small fraction of the regional landscape supports eastern hemlock. Thus, these disjunct populations represent small islands or target areas for HWA colonization. The probability of adelgids being transported by wind to these small eastern hemlock populations must be quite low even if HWA density is high near the southernmost contiguous extent of eastern hemlock. However, relatively large populations of eastern hemlock occur in the William B. Bankhead National Forest (BNF) of north Alabama. These larger populations at BNF represent larger islands of islands of suitable HWA habitat and thus, have a higher probability of being infested. If the HWA reaches these populations, the BNF may serve as a source for jump dispersal to other outlying eastern hemlock populations in Tennessee, Alabama, and Georgia.

Birds are also dispersal agents of the HWA. Adelgids have been documented on birds up to 2 km from the nearest known eastern hemlock individual (McClure, 1990). Adelgids have been documented on a variety of migratory bird species with varied foraging, nesting, and roosting behavior. It is hypothesized that HWA eggs and crawling nymphs can remain attached to birds during migration, including spring migration, which is a time when nymphs are most active (McClure, 1989b, 1990). Thus, birds may be the most effective agents for the long distance dispersal of adelgids. This may be especially true for specific avian species that favor eastern hemlock stands (e.g. black-throated green warbler (Dendroica virens Gmelin) and winter wren (Troglodytes troglodytes L.); Yamasaki et al., 1999). Also, larger populations of eastern hemlock, such as those at the BNF, represent larger target areas for migrating birds (Lomolino, 1990). However, birds have only been documented to transport HWA ca. 2 km from eastern hemlock stands (McClure, 1990). This distance is not sufficient to allow for the colonization of disjunct populations near the southern boundary of eastern hemlock.

**PERSISTENCE OF DISJUNCT POPULATIONS**

If disjunct eastern hemlock populations are not infested by the HWA, and biocontrol and other measures are not successful through the contiguous range, eastern hemlock may become restricted to the periphery of its current distribution and may be included with the number of other species whose ranges have collapsed in an explosive manner and are absent from the core of their historic range (see Channell and Lomolino, 2000b). If disjunct populations persist, they will become even more important centers of biodiversity for a variety of species, including terrestrial and aquatic species often associated with eastern hemlock stands (Yamasaki et al., 1999; Snyder et al., 2002). Even though these disjunct populations are often relatively small, persistent populations are not necessarily those with the highest densities, but those most isolated from the point of contact with an extinction force (Lomolino and Channell, 1995, 1998; Lomolino and Smith, 2001; Channell and Lomolino, 2000a, 2000b). Peripheral populations of eastern hemlock are viable and may provide opportunities to maintain the species. Thus, they should not be overlooked in control and conservation efforts even though many populations are relatively small.

**ACKNOWLEDGEMENTS**

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**LITERATURE CITED**


The most recent 100-year trend in global annual temperature is 0.7 °C. The continents have warmed more than the oceans, the northern hemisphere more than the southern hemisphere, and high latitudes more than low latitudes. Winter and spring have warmed more than summer or fall, and nights have warmed more than days. Trends in global annual precipitation are more complex, but they have increased overall. There is also evidence for changes in some extreme events, such as warm temperatures, drought and heavy rain events, and midlatitude and tropical cyclones (Trenberth et al., 2007).

Future climate projections suggest that these trends will continue as humans continue to increase atmospheric concentrations of greenhouse gases. According to various climate models, the likely temperature increase over the next century could be anywhere between 1.1 and 6.4 °C, depending on the greenhouse gas emission scenario (Solomon et al., 2007).

Studies have also been carried out for the United States. The National Assessment Synthesis Team (NAST) report concluded that United States temperature and precipitation trends were similar to those for the globe as a whole. Over the twentieth century the temperature trend was 0.6 °C. Precipitation trends again were complex, but most regions experienced an increase (McCracken et al., 2001). Regionally there was variation in these trends. The southeastern United States was the only region to experience a cooling trend. It also experienced some of greatest increases in precipitation. Future climate projections again suggest a continuation of these trends. In the southeast, the cooling is projected to change to a warming. Changes in precipitation are less clear (Burkett et al., 2001; McCracken et al., 2001).

Many studies of climate change in the United States have been conducted recently using the USHCN data set. Most have been consistent with the findings already reviewed, although the magnitude of some of the trends has varied (Karl et al., 1995, Hansen et al., 2001). A recent study using a subset of the full data set, with stations chosen based on long periods of record and lack of missing data, reported a slightly larger temperature trend of 0.8 °C per century, with seasonal trends of 1.2, 0.9, 0.7, and 0.5 °C for winter, spring, summer, and fall, respectively. Regionally, the southeast still shows some cooling, but by no means over the whole region. In Alabama, the cooling is apparent only in some seasons, and only in the central eastern and Gulf Coast parts of the state (Lu et al., 2005).

Other studies have suggested problems with the USHCN data set. They argue that the data includes poorly sited stations and problems with observation techniques, with documentation on station changes such as location and instrumentation and with the corrections applied to the data to account for these changes. In some cases these problems can significantly affect analysis carried out with the data, especially at the local level (Christy, 2002; Daly et al., 2007; Pielke et al., 2007).

**MATERIALS AND METHODS**

The USHCN data set (National Climatic Data Center, 2008) consists of daily and monthly temperature and precipitation records from approximately 1200 weather stations within the contiguous United States. The data set was developed specifically to study climate change in the United States at the national and regional level. The station records were chosen based on length of record, spatial coverage, and the completeness of the data. Despite some of the problems listed above, this is still one of the best data sets available for the analysis undertaken here.

The records have been checked for accuracy and adjusted where necessary. Erroneous data has been removed, and missing data has been estimated where possible using surrounding stations. Data has been adjusted for changes in observation times, instruments, station moves, and urban warming. The start date varies between stations, but most stations have records starting around 1900 and ending in 2005.

This study uses monthly USHCN data. There are 15 stations in the USHCN data set in Alabama, located in every part of the state. They have various periods of record. All have monthly data up to 2005. Some stations have records dating from as early as 1882, one from as late as 1940.

Annual average temperature and total precipitation were calculated for this study from the monthly data. An annual value was calculated only if a station had all 12 monthly values for that year, to avoid biasing annual values in incomplete years.

Only 10 stations out of the original 15 have annual temperature and precipitation values for the majority of years for the period 1901 - 2000 and the majority of years in each decade in that period. These 10 stations were chosen for this study based on this period of record. The locations of these stations are shown in Fig. 1.

There is, of course, a compromise between temporal and spatial coverage in any climate change study. Choosing stations based primarily on their length of record means losing some records in parts of the state. Most of the stations are located in central and southern Alabama. There is only one in the northern part of the state, Valley Head, in the northeast, and no stations on the Gulf Coast. However, this compromise was necessary in order to study long term climate change.

In order to assess the changes in temperature and precipitation over the twentieth century, the 1901 - 2000 trends were calculated for each variable at each station. These were calculated using regression analysis on the temperature and precipitation time series. The slope of the regression line gives an annual trend. This was expressed per century to make it easier to compare with national and global trends.

This type of trend analysis is a relatively common way of expressing change in a climate variable, but does not give any information on changes in climate normals, the average climate a person would expect to experience in a given place over a given time period. For this reason, climate normals were calculated for standard 30-year periods at the beginning and end of the record, 1901 - 1930 and 1971 - 2000. Both means and standard deviations were calculated to assess the climate of each period and its variability.

Hypothesis tests were carried out to see if there were any differences in the means of each variable at each station between the two climate normals periods. These were calculated using two sample T tests. Hypothesis tests were also carried out to see if there were any differences in the standard deviations. These were calculated using F tests. The results of the F tests were also used to determine whether to pool variances in the T tests.

The results of the analysis were considered significant if the slope of the trend
The same analyses were carried out on state time series. These time series were calculated using a standard climate division technique where the mean temperature or precipitation value in each division is calculated using every station in that division, then weighted according to the area of the division. This approach accounts for uneven spatial distribution of data (Guttman and Quayle, 1996).

**RESULTS**

The temperature results are shown in Table 1. The majority of stations show a decreasing trend in annual temperature. These trends are significant at many of those stations. The significant trends range from -0.6 to -1.0 °C. Geographically, the trend is fairly uniform. The only exceptions, stations showing a warming trend, were Gainesville and Greensboro in the central west part of the state, and Union Springs in the southeast, and the trends were not significant.

Changes in means were similar to trends, as might be expected. The majority of stations showed a decrease in their mean temperature, many a significant decrease. Geographically, the changes in the mean followed the same pattern as the trends.

There were no significant changes in standard deviations. Overall, the temperature results suggest temperature decreases over time over much of the state, with the expected change in average temperatures but no change in temperature variability.

The state temperature time series is shown in Fig. 2. It shows a cooling trend, with decadal variability. There are clear cool and warm periods. The beginning of the twentieth century up until the 1920s was a period of warming, the middle of the century a period of cooling, and the 1970s to the end of the century another period of warming. The temperature trend was significant at -0.6 °C. The mean temperature also decreased significantly and there was no significant change in the standard deviation.

The precipitation results are shown in Table 2. The majority of stations show an increasing trend in annual precipitation. These trends are significant at many of those stations. The significant trends range from -37.3 to 36.8 cm. Geographically, the trend is fairly uniform. The exceptions were Troy, in the central east part of the state, which showed no trend in precipitation, and Union Springs, in the southeast part of the state, and Valley Head, in the northeast part of the state, which showed a significant drying trend.

Again, changes in means were similar to trends. The majority of stations showed an increase in their mean precipitation, many a significant increase. Geographically, the changes in the mean followed approximately the same pattern as the trends. Exceptions were Thomasville, in the southwest part of the state, which showed a significant change in the mean, but no significant trend, and Union Springs, which showed a significant trend, but no significant change in the mean.

There was one significant trend in standard deviation at Union Springs, where the standard deviation had decreased significantly. Overall, the precipitation results suggest increases in precipitation over time over much of the state, with the expected changes in average precipitation but no changes in precipitation variability. An interesting exception to this is one station in the southeast part of the state, which showed the opposite results.

The state precipitation time series is shown in Fig. 3. It shows a wetting trend, with annual variability. Cycles of dry and wet periods are less clear, but there are clearly drier and wetter years. The precipitation trend was not significant, neither were changes in the mean or standard deviation.
Table 1. Annual temperature results, 1971-2000 means and standard deviations, change in means and standard deviations between 1901-1930 and 1971-2000, and trends from 1901-2000. Units are degrees Celsius. Results that are significant at the 5% level are indicated with an asterisk.

<table>
<thead>
<tr>
<th>Station</th>
<th>Mean</th>
<th>Change</th>
<th>Deviation</th>
<th>Change</th>
<th>Trend</th>
</tr>
</thead>
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<td>0.1</td>
<td>0.6</td>
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</tr>
<tr>
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<td>0.7</td>
<td>-0.1</td>
<td>0.3</td>
</tr>
<tr>
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<td>17.9</td>
<td>-0.4 *</td>
<td>0.6</td>
<td>-0.1</td>
<td>-0.6 *</td>
</tr>
<tr>
<td>Selma</td>
<td>18.2</td>
<td>-0.7 *</td>
<td>0.6</td>
<td>-0.1</td>
<td>-0.9 *</td>
</tr>
<tr>
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<td>0.6</td>
<td>-0.1</td>
<td>-1.0 *</td>
</tr>
<tr>
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<td>0.6</td>
<td>-0.1</td>
<td>-0.3</td>
</tr>
<tr>
<td>Troy</td>
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<td>-0.7 *</td>
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<td>-0.9 *</td>
</tr>
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</table>

Figure 2. Annual temperature for Alabama, 1901-2000, based on the United States Historic Climatology Network (USHCN) weather stations used in this study.

Table 2. Annual precipitation results, 1971-2000 means and standard deviations, change in means and standard deviations between 1901-1930 and 1971-2000, and trends from 1901-2000. Units are centimeters. Results that are significant at the 5% level are indicated with an asterisk.

<table>
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<th>Deviation</th>
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<th>Trend</th>
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<td>4.6</td>
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Figure 3. Annual precipitation for Alabama, 1901-2000, based on the United States Historic Climatology Network (USHCN) weather stations used in this study.
DISCUSSION

This study has addressed changes in temperature and precipitation in the state of Alabama over the twentieth century. As a whole, the state has experienced a decrease in annual temperatures and an increase in annual precipitation at the majority of weather stations. Many of the changes in temperature and precipitation have been significant, although there is no clear geographic pattern or spatial signal to these changes.

Climate normals at the beginning and end of this period give some insight into changes in the typical climate of the state. In line with the trends explained above, average temperature has decreased and average precipitation has increased in most places, with two exceptions at stations in the northeast and southeast parts of the state, where precipitation decreased significantly. There has been no change, however, in the variability of climate, with one exception, a station in the southeast part of the state where precipitation variability decreased significantly.

The major problem with the analysis presented here is the small number of stations in the state with a high quality climate record over a long time period. Ideally, more stations would be used to give a better and more even coverage of the state, especially north Alabama and the Gulf Coast. Despite this fact, the consistency of the results increases confidence in them, along with the fact that similar changes in climate have been detected across the southeastern United States.

Seasonal analysis may also reveal more detailed climate changes, and show what time of year most of the cooling or wetting is taking place, and whether there are any times of year when warming or drying is taking place. There is likely to be more monthly than annual variability, and this analysis would reveal that.

Many interesting questions remain: why did Alabama and the southeastern United States experience cooling rather than warming over the twentieth century? Will the global warming signal eventually override this cooling over the twenty first century or will certain regions like the Southeast continue to cool? These and other questions will only be answered with time and further analysis.

LITERATURE CITED


ABUNDANCE, IDENTIFICATION, AND PROSPECTIVE PARTICIPATION OF BACTERIA ON GOPHER TORTOISE SHELL DEGRADATION

Valerie M. Johnson¹, Craig Guyer¹, Matthew D. Shawkey², and Sharon R. Roberts¹
¹Department of Biological Sciences, 331 Funchess Hall, Auburn University, Auburn, AL 36849; ²Department of Biology and Integrated Bioscience Program, University of Akron, Akron, OH 44325

Corresponding Author: Johnson, V. M. (johnsvm@auburn.edu)

ABSTRACT

Shell degradation has been described, in one species of Gopherus, to be caused by an ingested environmental toxicant, and in another species of the same genus, to be caused by a topical fungus. Both studies document the presence of several bacterial species; however, these studies fail to specify if bacteria contribute to the degradation. Physical descriptions of the disease are analogous between species and similar to observations made here of a third Gopherus species. The purpose of the study was to test whether bacteria on tortoise shells can be associated with shell degradation. Between June and August 2002, bacteria were sampled from the centers and sulci of plastral scutes of nine gopher tortoises lacking signs of shell degradation (unaffected) and thirteen tortoises having signs of shell degradation (affected). Keratinolytic bacteria were approximately 36 times more abundant on tortoises displaying signs of degradation than on tortoises not displaying such signs. The bacterial flora capable of growing on tryptic soy agar and sampled from unaffected tortoises consisted of five species, three of which are likely to degrade keratin. The flora cultured from unaffected and affected tortoises display signs of degradation than on tortoises not displaying such signs. The bacterial flora capable of growing on tryptic soy agar and sampled from unaffected tortoises consisted of five species, three of which are likely to be capable of degrading keratin. The bacterial flora capable of growing on tryptic soy agar and sampled from affected tortoises consisted of five species, two of which, Pseudomonas balearica and Stenotrophomonas maltophilia, are likely to degrade keratin. The flora from unaffected and affected tortoises contained one shared species, S. maltophilia. Thus, affected tortoises contain a bacterial assemblage that differs from unaffected tortoises and the distribution of P. balearica and S. maltophilia suggests them to be possible causal or contributing agents of shell disease.

INTRODUCTION

Shell degradation has been documented in two North American tortoise species. In G. agassizii Cooper (desert tortoise), Jacobson et al. (1994) documented ingestion of a toxicant resulting in shell lesions causing degradation; however, biopsies revealed no abnormalities in the epidermal cell layer from which shell scutes are constructed. In Gopherus berlandieri Agassiz (the Texas tortoise), a fungus has been identified as an etiological agent of shell degradation (Rose et al., 2001). The fungus colonized the shell from the exterior environment and directly degraded keratin. Both authors document bacteria in the shell lesions and suggest that they were secondary invaders of the toxicant- or fungal-damaged tortoise shells. Morphological characteristics of shell degradation in the desert tortoise, Gopherus agassizii, include lesions and discolorations of the outermost shell layer (scutes)(Homer et al., 1998). Similar shell conditions exist in Gopherus polyphemus Daudin (gopher tortoises) in that scutes of some individuals are discolored (white, yellow, or orange) and degraded (V. M. J., pers. obs.) In both species, shell degradation can be found on the carapace and plastron, although it is more prevalent on the plastron (Jacobson et al., 1994; Johnson, 2004).

Although a variety of bacteria likely live on gopher tortoises, those that primarily degrade keratin would most likely be associated with shell degradation because the scutes that comprise the outer shell layer are composed of keratin. Gopher tortoise plastrons (the bottom portion of shells) are continually in close contact with warm, damp soil because these turtles use burrows as general refugia (Auffenberg, 1969). This environment provides ideal growing conditions for mesophilic bacteria (Ullsch and Anderson, 1986; Muza et al., 2000; Nester et al., 2001). Keratin-degrading bacteria have been isolated from soil and bird feathers, and at least four genera contain species capable of digesting β-keratin (Noval and Nickerson, 1959; Williams et al., 1990; Burtt and Ichida, 1999; Shawkey et al., 2003). Turtle scutes are modified scales (Kardong, 2006), suggesting that the structural framework of the turtle scute is β-keratin (Fraser and Parry, 1996; Parry and North, 1998).

Our primary goal was to determine if bacterial abundance and identity differed for samples from the plastrons of unaffected (those lacking shell degradation) and affected (those exhibiting shell degradation) gopher tortoises. This was performed as a preliminary assessment of the potential role of bacteria in causing shell degradation. A secondary goal was to determine whether bacterial abundance differed between scute centers and sulci (the growth zones between scutes). This was used to assess the potential avenue of invasion of shell bacteria. Because keratin is transported to scutes via capillaries under the scute sulci (Pough et al., 2001), increased abundance of bacteria along sulci would be consistent with a systemic invasion of scutes by bacteria. Increased abundance of bacteria at scute centers would be inconsistent with this avenue of invasion.

MATERIALS AND METHODS

Field Methods

Samples were collected from June through August 2002 on one study site located within the DeSoto National Forest, Forrest County, Mississippi (31°11.26′N, 89°1.57′W(WGS 84/NAD83)(Figure 1). The soils at this site were a loamy sand mixture of both the McLaurin and Heidel series (Davis and Byers, 1979). Tortoises were captured in Tomahawk® wire traps shaded with burlap to prevent heat exhaustion. The shell of each captured animal was classified either as degraded (affected) or not degraded (unaffected). An affected tortoise was defined as having at least 1.0 mm² of flaking or chipping of at least one scute while an unaffected tortoise had no flaking or chipping (Figure 2). Thirteen affected tortoises were sampled, nine males (mean carapace length (CL) = 242 mm) and
four females (mean CL = 276 mm). Nine unaffected tortoises were sampled four males 
(mean CL = 233 mm) and five females (mean CL = 240 mm). After a tortoise was removed 
from a trap, the plastron was brushed by hand and rinsed with approximately 3-5 ml of 
phosphate-buffered saline (PBS) to remove fine particulate matter. Two samples were 
taken with sterile BBL™ culture swabs, immersed in sterile PBS before use. The first swab 
was used to sample the central portion of 2-3 plastral scutes. Samples from unaffected 
tortoises were taken from non-degraded scutes, and samples from affected tortoises were 
taken from degraded areas on 2-3 plastral scutes. The second swab was used to collect 
samples from 2-3 sulci between plastral scutes. The sulci were sampled because they are 
lines of active growth of the shell. To standardize sampling, sulci of affected and unaffected 
tortoises were sampled from areas not affected by shell disease. All samples were collected 
using individual swabs that were replaced into their respective sterile plastic tubes prior to 
storage in a cooler with ice. The swabs were kept on ice for the remainder of the day (up 
to six hours) until placed in a refrigerator where they remained for up to seven days before 
being shipped overnight on ice to Auburn University for further analysis.

**Bacteria on Gopher Tortoise Shells**

This medium produced keratinase, an enzyme that catalyzes hydrolysis of keratin (Shawkey 
et al., 2003). Therefore, most bacteria grown on FMA should have been able to digest 
keratin and were therefore, considered keratin degrading. Both media contained 100 µg/ml 
of cycloheximide to inhibit fungal growth (Smit et al., 2001).

Each swab was washed in 1 ml of sterile PBS and diluted (1:1000) to produce 
countable plates using the spread-plate method. One hundred microliters of each dilution 
was plated onto a petri dish containing TSA and another 100 µl was plated on a petri 
dish containing FMA. Samples were incubated at 37 °C (see Johnston, 1996) for 48 hrs 
(TSA) or 14 days (FMA). The standard plate count method was used to determine the total 
number of colony-forming units (CFUs) of each sample (Nester et al., 2001). Negative 
control plates were inoculated with sterile PBS during each sample-processing period. No 
growth was observed on these plates.

**Identification of Bacteria**

Fifty total colonies from both TSA and FMA having unusual or infrequently 
detected morphologies were chosen to increase the probability of obtaining a diverse 
sample of bacterial taxa. Colonies were re-streaked on at least three plates containing TSA 
and these were incubated at room temperature for 72 hrs until the purity of a culture was 
confirmed by observation of consistent colony morphology on all three replicate plates. 
Pure cultures were re-streaked on TSA and incubated at 28 °C for 48 hrs to prepare them 
for identification. A loopful of cells was harvested, and gas chromatography of cellular fatty 
acids was used to identify bacteria (Sasser, 2001). Samples were analyzed using a Hewlett-
Data Analysis

A total of 44 samples (two from each tortoise) were collected from nine unaffected tortoises and 13 affected tortoises. Differences in bacterial load between categories of agar type (TSA and FMA) and tortoise condition (unaffected and affected) were compared using a two-way repeated measures (scute and sulcus) analysis of variance (ANOVA) implemented in SPSS (Statistical Package for the Social Sciences, 11.0 for Windows). Alpha was set at 0.05. Because sample location (sulcus vs scute) was not recorded for seven samples, a total of 30 samples, 16 from unaffected tortoises (eight individuals, each sampled at scute center and along scute sulci) and 14 from affected tortoises (seven individuals, each sampled at scute center and along scute sulci) were used for this analysis. EstimateS (Colwell, 2004) was used to estimate the total number of sampled bacteria on affected and unaffected tortoises and to compare overall similarities of these two fauna. All 30 samples were used in the analysis.

RESULTS

Bacterial loads on TSA (1.32 x 10^5 ± 1.92 x 10^6 cfu/ml) were approximately four times larger than those on FMA (3.50 x 10^5 ± 8.96 x 10^5 cfu/ml) medium (F = 10.6, p = 0.003; df = 1). Overall, bacterial loads were approximately 42 times greater on affected than unaffected tortoises (F = 28.6; p < 0.001; df = 1). However, the difference in bacterial loads between affected and unaffected tortoises was significantly more pronounced for bacteria grown on TSA than on FMA (F = 9.9; p = 0.004; df = 1). Bacterial loads from TSA were approximately 46 times greater on affected than unaffected tortoises, whereas bacterial loads from FMA were approximately 36 times greater on affected than unaffected tortoises. Thus, affected tortoises had relatively greater abundances of bacteria of all types, and proportionately fewer keratinolytic bacteria on their shells than unaffected tortoises. Location of the sample (scute and sulcus) was inconsequential either alone (F = 0.001; p = 0.97; df = 1) or in interaction with tortoise condition and agar type (F = 0.25; p = 0.62; df = 1).

Table 1. Bacteria isolated from shells of gopher tortoises captured on the DeSoto National Forest, Forrest County, Mississippi. Growth treatments are tryptic soy agar (TSA) and feather meal agar (FMA). Bacteria were identified using gas chromatography of cellular fatty acids. Keratin degrading status is coded as (1) genus known to degrade keratin, (2) genus not known to degrade keratin but grew on FMA in this study, and (3) genus not known or observed to degrade keratin. Affected tortoises (N = 13) had at least one area of chipping or flaking on at least one scute, unaffected tortoises (N = 9) had no chipping or flaking of scutes.

### Bacteria on Gopher Tortoise Shells

<table>
<thead>
<tr>
<th>Bacterial Species</th>
<th>Keratin degrading status</th>
<th>Number of isolates on TSA</th>
<th>Number of isolates on FMA</th>
<th>Tortoise Condition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pseudomonas balearica</td>
<td>1</td>
<td>6</td>
<td>2</td>
<td>Affected</td>
</tr>
<tr>
<td>Stenotrophomonas maltophilia</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>Affected</td>
</tr>
<tr>
<td>Enterococcus faecalis</td>
<td>3</td>
<td>6</td>
<td>0</td>
<td>Affected</td>
</tr>
<tr>
<td>Enterococcus cancerogenus</td>
<td>2</td>
<td>4</td>
<td>1</td>
<td>Affected</td>
</tr>
<tr>
<td>Klebsiella pneumoniae</td>
<td>2</td>
<td>6</td>
<td>1</td>
<td>Affected</td>
</tr>
<tr>
<td>Kocuria carniphilia</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>Unaffected</td>
</tr>
<tr>
<td>Salmonella typhimurium</td>
<td>3</td>
<td>3</td>
<td>0</td>
<td>Unaffected</td>
</tr>
<tr>
<td>Staphylococcus sciuri</td>
<td>1</td>
<td>5</td>
<td>2</td>
<td>Unaffected</td>
</tr>
<tr>
<td>Pseudomonas aeruginosa</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>Unaffected</td>
</tr>
<tr>
<td>Stenotrophomonas maltophilia</td>
<td>2</td>
<td>6</td>
<td>1</td>
<td>Unaffected</td>
</tr>
</tbody>
</table>

Of fifty colonies that we selected to maximize total diversity, only nine bacterial species were found. Between unaffected and affected tortoises, each flora was nearly completely different in composition from the other. Four bacterial species were exclusive inhabitants of unaffected tortoises, four were exclusive inhabitants of affected tortoises, and one was found on both categories of tortoises (Table 1). The number of bacterial species capable of growing on TSA and FMA and present on affected tortoises was estimated to be 5.0; the number of such bacterial species from unaffected tortoises was estimated to be 4.5. Thus, our observed samples represented 90% of the species likely to be present on tortoises and capable of growing on TSA and FMA.

DISCUSSION

Four species, Kocuria carniphilia (formerly K. varians; Tvrzova et al., 2005), Staphylococcus sciuri, Salmonella typhimurium, and Pseudomonas aeruginosa, were found only on unaffected tortoises. One of these, Salmonella typhimurium, is not known to degrade keratin, but was not observed to grow on FMA. The other three are known to degrade keratin, but were not observed on affected gopher tortoises. Thus, these bacterial species are unlikely to cause or contribute to shell disease in gopher tortoises. Instead, these bacteria appear to be relatively benign in their actions on gopher tortoises, as they generally are on other potential hosts (Mader, 1996; Silvanose et al., 2001; Adegoke, 2003; Tvrzova et al., 2005).

Four species were found only on affected tortoises, Enterococcus cancerogenus, Klebsiella pneumoniae, Enterococcus faecalis, and Pseudomonas balearica. One of these, Enterococcus faecalis, is not known to degrade keratin and was not observed to grow on
Bacteria on Gopher Tortoise Shells

FMA. Thus, this species is unlikely to cause shell degradation, but apparently invades bacterial communities only of affected tortoises. It is also reported as part of the normal flora of humans (Nester et al., 2001). The other three species are known to degrade keratin or were observed to grow on FMA, suggesting that they might be capable of causing or contributing to the shell degradation found on the study animals. However, Enterococcus is known to be part of the normal flora of bog turtles (Brenner et al., 2002) and Klebsiella pneumoniae is part of the normal flora of reptiles (Mader, 1996). Therefore, they seem unlikely causes of shell degradation since they should cause similar degradation in all host reptiles. This leaves P. balaerica, a species described from wastewater and marine sediment samples of the Balearica Islands near Spain and capable of growing at extremely high temperatures (46°C; Bennasar et al., 1996). Pseudomonas balaerica deserves additional study as a possible causative agent of shell disease because it is known to degrade keratin and is associated only with affected individuals.

Only one species of bacteria, Stenotrophomonas maltophilia, was found on both unaffected and affected gopher tortoises. Colonies isolated from unaffected animals were shown to be keratinolytic. This species of bacteria has been reported from anacondas (Miller et al., 2004) and West African dwarf crocodiles (Harris and Rogers, 2001), but is not known to have deleterious effects on those reptiles. Thus, the bacterial species has keratinolytic activities and a distribution pattern on unaffected and affected tortoises that make it a candidate for causing shell degradation in gopher tortoises.

No difference in keratinolytic bacterial loads was observed between scute centers and sulci, a result consistent for both affected and unaffected tortoises. Thus, keratinolytic bacteria affected tortoises in a fashion consistent with external rather than internal invasion of the shell. These species might have served as the primary etiological agents of shell disease in gopher tortoises. Alternatively, because physical descriptions of the shell degradation on desert tortoise shells were similar to those described here for gopher tortoises, keratinolytic bacteria may have colonized shells damaged first by environmental contaminants (Jacobson et al., 1994). No fungal tests were performed. Some species of fungi have been reported to cause shell disease in Texas tortoises, while others cause shell disease in the Spur-thighed tortoise, G. agassizii (Rose et al., 2001). A fungal primary agent could have been the causative agent of shell disease in gopher tortoises, and if this were the case, keratinolytic bacteria then would function as secondary invaders associated with a primary agent.

Shell degradation has been reported from all North American tortoise species except Gopherus flavomarginatus Legler (the Bolson’s tortoise). Further research may determine whether shell degradation is a common sign of three distinct maladies (toxicant, fungus, and keratinolytic bacteria) or a single malady (environmental stress) leading to two proximate manifestations (fungal and bacterial). Bacteria were present on G. agassizii shells (Jacobson et al., 1994), and further studies concerning the location, concentration, and identity of keratinolytic bacteria are warranted by the findings presented here. Likewise, general histological studies of G. polyphemus are needed to examine scute tissue formation in association with shell degradation. Finally, samples of fungi from shells of G. agassizii and G. polyphemus should be isolated and referenced against the fungus isolated from G. berlandieri (Rose et al., 2001).

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LITERATURE CITED


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PTERIDOPHYTES OF SOUTHEAST ALABAMA: DICHOTOMOUS KEYS, ILLUSTRATIONS AND DISTRIBUTION MAPS

Michael Woods and Alvin R. Diamond, Jr.
Department of Biological and Environmental Sciences
Troy University
Troy, Alabama 36082

Correspondence: Woods, Michael (mwoods@troy.edu)

ABSTRACT

This treatment includes all species of pteridophytes known to occur naturally and those that have become naturalized in southeast Alabama. A total of seventeen families, twenty-nine genera, fifty-nine species, two varieties, and four hybrid taxa are known to occur in the study area. Dichotomous keys are provided for all families, genera, species, and three of the hybrids. A description is provided for the remaining two varieties and one hybrid. County level distribution maps and illustrations are provided for all species. The area delineated as southeast Alabama includes Barbour, Butler, Coffee, Conecuh, Covington, Crenshaw, Dale, Escambia, Geneva, Henry, Houston, and Pike counties. Distribution records are based upon specimens deposited in the Troy University Herbarium (TROY), J. D. Freeman Herbarium (AUA), The University of Alabama Herbarium (UNA), and University of West Florida Herbarium (UWFP).

INTRODUCTION

Diamond and Woods (2007) discussed the history of the literature dealing with pteridophytes of Alabama, and also provided a description, including geology, topography, watersheds, and climate of the twelve counties in the southeastern section of the state that comprise the study area (Barbour, Butler, Coffee, Conecuh, Covington, Crenshaw, Dale, Escambia, Geneva, Henry, Houston, and Pike Counties). They provided a dichotomous key to the seventeen families and a checklist of the fifty-nine species, and three hybrid taxa known to occur in the study area.

The objectives of this treatment were to expand on the earlier publication and to develop dichotomous keys, not only for the families but for all species of pteridophytes known to occur naturally, and those that have become naturalized in southeast Alabama. Also provided in this treatment are descriptions for each genus, and illustrations, county level distribution maps, and habitats for each species.

MATERIALS AND METHODS

The dichotomous keys and descriptions are based upon material deposited in the herbarium of Troy University (TROY) and descriptions provided by Snyder and Bruce (1986). Distribution records are based upon specimens deposited in the Troy University Herbarium (TROY), J. D. Freeman Herbarium (AUA), The University of Alabama Herbarium (UNA), and University of West Florida Herbarium (UWFP). Additional distribution data were obtained from Jack Short (pers. com.). With the exception of Isoetaceae and Lycopodiaceae, the nomenclature follows Flora of North America (Flora of North America Editorial Committee, 1993).

RESULTS AND DISCUSSION

Pteridophytes of southeast Alabama are represented by seventeen families, twenty-nine genera, fifty-nine species, two varieties, and four hybrid taxa. Dryopteridaceae, the largest family, is represented by seven genera, nine species and one hybrid; Thelypteridaceae by three genera and seven species; Pteridaceae by three genera, six species and one variety; Ophioglossaceae by two genera and eight species; Lycopodiaceae by two genera, six species and three hybrids. Isoetaceae is represented by one genus and seven species. The families Aspleniaceae, Blechnaceae, Osmundaceae, and Selaginellaceae are represented by one genus and two species each. Dennstaedtiaceae is represented by one genus and one variety.

The families Azollaceae, Equisetaceae, Marsileaceae, Polypodiaceae, and Salviniaceae are represented by a single species each. Thirteen species, or 22.4% of the taxa, are non-native.

The collection of Polystichum braunii (Spnner) Fée from Dale County represents the first collection of this species in the southern one-half of the United States (Woods and Diamond, 2006). This taxon is native to northeastern and coastal northwestern North America where it typically grows in cool, moist, shaded places in boreal forests and northern deciduous woods. Although the Dale County population is likely an escape from cultivation, no homes occur in the immediate vicinity of the collection site.

Lycopodium digitatum Dillenius ex A. Braun is known from two counties in the study area, Barbour and Escambia. The Barbour County population represents an extension of the natural range of this taxon by approximately 120 km south. However, the Escambia County population is possibly introduced. The site where it was collected is an area of a cemetery where flora arrangements have been discarded for many years. In addition, this site is approximately 300 km southwest from the nearest population.

Since Diamond and Woods (2007), one additional taxon has been found to occur in the study area. Botrychium jenmanii (L.) Underwood (Alabama grape fern) has been reported from Escambia County. The collection was made by James Burkhalter (#18178) on January 5, 2002 and is deposited in the herbarium at the University of West Florida (UWFP). In addition, one taxon, Asplenium trichomanes Linnaeus, reported by
Woods and Diamond (2007) based on a single collection made from the study area was recently annotated by Jack Short to *A. resiliens* Kunze and, therefore, removed from this treatment.

**KEY TO PTERIDOPHYTE FAMILIES**

1. Aerial stems hollow, jointed................................................................................................. 1. Equisetaceae

1. Aerial stems absent or solid, not jointed ................................................................................. 2

2. Leaves linear; stems a corn .................................................................................................. 2. Isoetaceae

2. Leaves broad or reduced scale-like structures; stems a rhizome or stolon......................... 3

3. Plants aquatic, free floating or rooted in mud................................................................. 4

3. Plants terrestrial.................................................................................................................. 5

4. Photosynthetic leaves 4-parted and clover-like, petioles widely spaced on long creasing stems at least partly rooted in substrate .............................................. 3. Marsileaceae

4. Photosynthetic leaves round or oval, not clover-like, petioles closely spaced on short free floating stems......................................................................................... 5

5. Leaves glabrous adaxially .................................................................................................. 4. Azollaceae

5. Leaves pubescent adaxially .................................................................................................. 5. Salviniaceae

6. Plants moss-like in appearance; leaves <1 cm long ............................................................ 7

6. Plants not moss-like; leaves >1 cm long .............................................................................. 8

7. Plants slender; sterile leaves dimorphic, ligulate; heterosporous ................................. 6. Selaginellaceae

7. Plants coarse; sterile leaves monomorphic, ligulate; homosporous ................................. 7. Lycopodiaceae

8. Leaves with rachis twining, climbing, vine-like .................................................................. 8. Lygodiaecae

8. Leaves erect, without a rachis or a short rachis, not twining, not vine-like .............. 9

9. Sporangia 0.5-1.0 mm in diameter; roots tuber-like, thick, fleshy ................................. 9. Ophioglossaceae

9. Sporangia 0.08-0.1 mm in diameter; roots wiry......................................................... 10

10. Stems short, erect, stout; roots matted, wiry ................................................................. 10. Osmundaceae

10. Stems elongated rhizomes, creeping; roots scattered....................................................... 11

11. Sori marginal, under revolute margins of blade; indusia absent................................. 12

11. Sori medial or submarginal but not under revolute margins of blade; indusia present or absent................................................................. 13

12. Rachis winged; pinnules opposite, >2.5 cm long ......................................................... 11. Dennstaedtiaceae

12. Rachis not winged; pinnules alternate, <2.5 cm long ...................................................... 12. Pteridaceae

13. Sori naked......................................................................................................................... 14

13. Sori with indusia................................................................................................................. 15

14. Fronds >30 cm long, glands and/or stipitate hairs present, peltate scales absent abaxially; sori <0.5 mm in diameter................................................................. 13. Thelypteridaceae

14. Fronds <25 cm long, glands and stipitate hairs present, peltate scales present abaxially; sori >1.0 mm in diameter................................................................. 14. Polypodiaceae

15. Sori elongate, in 1 row on each side and immediately adjacent to costae or costules.................................................................................................................. 15. Blechnaceae

15. Sori elongate to round, many per pinna, if elongate and parallel to costae then not immediately adjacent to them........................................................................................................ 16

16. Petioles with 1 x-shaped or 2 back to back c-shaped vascular bundles; sori on one side of a vein........................................................................................................ 16. Aspleniaceae

16. Petioles with 2 u-shaped or 2-many circular vascular bundles arranged in an arch; sori at least partially on two sides of a vein................................................................. 17

17. Adaxial surface of leaves pubescent, trichomes transparent; blade scales absent; petioles with 2 u-shaped vascular bundles......................................................... 13. Thelypteridaceae

17. Adaxial surface of leaves glabrous; blade scales present or absent; petioles with 2-many circular vascular bundles arranged in an arch................................. 17. Dryopteridaceae

1. EQUISETACEAE Michaux ex DeCandolle

**EQUISETUM** Linnaeus

Horsetail or Scouring Rush

Rhizomes with nodal buds; aerial stems green with whorls of reduced, nonfunctional leaves; internodes hollow; strobili terminal.

1. *E. hyemale* Linnaeus - SMOOTH SCOURING RUSH. Figure 1a, 1b. Banks of rivers and streams, seeps. Often associated with limestone.

2. ISOETACEAE Reichenbach

**ISOETES** Linnaeus

Quillworts

Plants arising from the ground in tufts; stems a corn; leaves quill-like, 1-3 dm long and 1-3 mm wide; heterosporous with sporangia on the adaxial leaf bases.

1. Sporangia solid white or hyaline ....................................................................................... 2

1. Sporangia white or hyaline with brown streaks or spots ................................................ 3

2. Velamen covering 100% of sporangia ............................................................................. 1. *I. flaccida*

2. Velamen covering <100% of sporangia........................................................................... 2. *I. valida*

3. Microspores white to pale tan, tuberculate .................................................................... 3. *I. appalachiana*

3. Microspores light gray to brown, papillose to spinulose ................................................. 4

4. Plants terrestrial or in seasonal pools or streams............................................................. 4. *I. melanopoda*

4. Plants submerged or emergent aquatics......................................................................... 5

5. Megasporos brown............................................................................................................ 5. *I. louisianensis*

5. Megasporos white............................................................................................................. 6

6. Microspores with prominent broad based spines ................................................................ 6. *I. hymalis*

6. Microspores papillose...................................................................................................... 7. *I. boomii*

1. *I. flaccida* A. Braun - Our species is represented by var. *chapmanii* Engelmann.

**FLORIDA QUILLWORT.** Figure 1c, 1d. Emergent or in shallow water of sand bottomed creeks or ponds.
2. *I. valida* (Engelman) Clute - ENGLERMANN’S QUILLWORT. Figure 1e, 1f. Shallow, sand bottomed creeks.

3. *I. appalachiana* D. F. Brunton & D. M. Britton - APPALACHIAN QUILLWORT. Figure 2a, 2b. Submerged to emergent along creek banks, woodland pools and lakes in sand, clay, or gravel substrates.

4. *I. melanopoda* Gay & Durieu – BLACK-FOOTED QUILLWORT. Figure 2c, 2d. Terrestrial or seasonally dry pools and streams.

5. *I. louisianensis* Thieret - LOUISIANA QUILLWORT. Figure 2e, 2f. Emergent along creeks and swamps with clay or sand substrates.

6. *I. hyemalis* D. F. Brunton - EVERGREEN QUILLWORT. Figure 3a, 3b. Shallow, running water in creeks and along river banks.

7. *I. boomii* Luebke – BOOM’S QUILLWORT. Figure 3c, 3d. Flowing water in low woods.

3. MARSILEACEAE Mirbel

   MARSILEA Linnaeus

   Water-clover

   Aquatic or amphibious, stems creeping with adventitious roots from nodes and internodes; leaves heteromorphic (photosynthetic and fertile), petioles filiform, blades palmately divided into 4 pinnae; sporocarps horizontal to strongly ascending near base of petioles.

   1. *M. minuta* Linnaeus – DWARF WATER-CLOVER. Figure 3e, 3f. Shoreline and shallow water along margin of beaver pond. Introduced.

4. AZOLLACEAE Wettstein

   AZOLLA Lamarck

   Mosquito fern

   Aquatic; roots threadlike, up to 5 cm long; stems dichotomously branched forming rotund to oblong plants about 1-3 cm in diameter; fronds minute, bilobed, pubescent, green to reddish-green.

   1. *A. caroliniana* Willdenow - MOSQUITO FERN. Figure 4a, 4b. Swamps, ponds and streams.

5. SALVINACEAE Reichenbach

   SALVINIA Séguiер

   Floating fern

   Floating aquatic, roots absent; leaves 3, dimorphic, 2 green, sessile, entire, floating and 1 finely dissected, petiolate, rootlike, submerged; sporocarps chainlike on submerged leaf.

   1. *S. minima* Baker – FLOATING FERN. Figure 4c, 4d. Still or stagnant waters of slow streams or ponds. Introduced.

6. SELAGINELLACEAE Willkomm

   SELAGINELLA Beauvois

   Spike-moss

   Stems creeping close to the ground to erect, sometimes forming large dense mats, often occurring as individual stems on clay banks; leaves in 4 rows, margins finely toothed; heterosporous with terminal strobili 1-2 cm long, 4-angled.

   1. Plants erect or creeping, not mat forming; microphylls with 1-2 rows of transparent marginal cells................................................................. 1. *S. apoda*

   2. Plants creeping, mat forming; microphylls with 3-5 rows of transparent marginal cells................................................................. 2. *S. ludoviciana*

   2. *S. apoda* (Linnaeus) Spring - MEADOW SPIKE-MOSS. Figure 4e, 4f. Moist shady areas, grassy margins of streams, clay banks.

   2. *S. ludoviciana* (A. Braun) A. Braun - GULF SPIKE-MOSS. Figure 5a, 5b. Swamps, stream banks, roadside ditches, moist ravines of calcareous ledges.

7. Lycopodiaceae Mirbel

   Plants terrestrial, on rocks or epiphytic; rhizomes normally present, erect stems simple or branched; leaves appressed to ascending or spreading; sporangia in strobili.

   In *Flora of North America* (Flora of North America Editorial Committee, 1993), the taxa covered in this family from Alabama are placed in the genera *Diphasiastrum*, *Lycopodiella*, *Palhindaea* and *Psuedolycopodiella*. The authors believe the taxonomy followed in this treatment is a better representation of the Lycopodiaceae in Alabama.

   1. Strobili sessile or pedunculate; peduncles, if present, bearing remote, reduced leaves; leafy stems primarily erect; leaves rigid, evergreen, dark green .......... 1. *Lycopodium*

   2. Strobili erect on leafy peduncules (non-leafy peduncles in *L. caroliniana*) or nodding or pendent on lateral shoots; peduncle, if present, bearing closely spaced, unreduced leaves; leafy stems prostrate or erect; leaves soft, deciduous, pale green; leafy stems prostrate or erect ................................................. 2. *Lycopodiella*

   1. *Lycopodium* Linnaeus

   Rhizomes or stems prostrate, with erect, regularly branching stems; leaves of prostrate stems appressed to ascending, linear to narrowly lanceolate, 1.8-4.6 mm long, leaves of erect stems appressed with decurrent bases, subulate, 1.8-3.5 mm long; strobili 2-4 per upright shoot, 1.4-4.0 cm long.
1. *L. digitatum* Dillenius ex A. Braun – SOUTHERN RUNNING-PINE. Figure 5c, 5d. Synonym is *Diphasiastrum digitatum* Dillenius ex A. Braun in Flora of North America (1993). Hardwood forests or open fields. The Escambia County population is possibly introduced.

2. **LYCOPODIELLA** Holub

   Rhizomes or stems prostrate, creeping, some with erect stems unbranched or branched; leaves needlelike to narrow, some 3-6 mm long; fertile shoot erect; strobili 0.5-8.0 cm long, pendulous or erect.

1. Upright stems branched; strobili pendulous from tips of lateral branches 1. *L. cernua*

2. Upright stems not branched; strobili erect from tips of upright shoots ................ 2

   2. Sporophylls broader than sterile, linear microphylls .............................. 2. *L. caroliniana*

   2. Sporophylls and sterile microphylls similar in shape, narrow lance-linear...........3

3. Sporophylls and microphylls appressed; strobili <10 mm thick ...................... 4

4. Strobili 3.0-4.9 mm wide; rhizomes <6 mm thick .................................. 3. *L. appressa*

5. Strobili 5-9 mm wide; rhizome >6 mm thick ......................................... 4. *L. x brucei*

6. Stolons flat on ground .............................................................................. 5. *L. prostrata*

7. Stolons arching .........................................................................................6

8. Peduncles <4 mm wide; sporophylls wide spreading.............................. 6. *L. alopecuroides*

9. Peduncles >4 mm wide; sporophylls ascending to spreading ..................... 7

10. Microphylls of erect stems spreading at 45 degrees; strobili 4-12 mm wide..... *L. x copelandii*

11. Microphylls of erect stems ascending at 30 degrees; strobili 10-20 mm wide................. 8. *L. alopecuroides x prostrata*

1. *L. cernua* (Linnaeus) Pichi Sermolli - NODDING CLUBMOSS. Figure 5e, 5f. Synonym is *Pallinheua cernua* (Linnaeus) Vasconcellos & Franco in Flora of North America (1993). Roadside ditches and old borrow pits. Introduced.

2. *L. caroliniana* (Linnaeus) Pichi Sermolli - CAROLINA CLUBMOSS. Synonym is *Pseudolycopodiella caroliniana* (Linnaeus) Holub in Flora of North America (1993). Figure 6a, 6b. Moist, sandy soils and wet clay banks along roadsides.

3. *L. appressa* (Chapman) Cranfill - SOUTHERN CLUBMOSS. Synonym is *Lycopodiella appressa* (Chapman) Cranfill in Flora of North America (1993). Figure 6c, 6d. Wet, sandy roadways or clay roadside ditches, shorelines.

4. *L. x brucei* Cranfill – BRUCE’S CLUBMOSS. Figure 6e, 6f. Roadside ditches, shorelines, bogs. A hybrid between *L. appressa* and *L. prostrata*.


6. *L. alopecuroides* (Linnaeus) Cranfill - FOXTAIL CLUBMOSS. Synonym is *Lycopodiella alopecuroides* (Linnaeus) Cranfill in Flora of North America (1993). Figure 7c, 7d. Wet, sandy field depressions, roadsides and clay roadside ditches.

7. *L. x copelandii* (Eiger) Cranfill – COPELAND’S CLUBMOSS. Figure 7e, 7f. Bogs, marshes, roadside ditches. A hybrid between *L. appressa* and *L. alopecuroides*.

8. *L. alopecuroides* (Linnaeus) Cranfill x *prostrata* (R. M. Harper) Cranfill – HYBRID CLUBMOSS. Figure 8a, 8b. Acidic sandy soils, wet ditches, wet pine woodlands.

9. **OPHIOGLOSSACEAE** C. Agardh

   The most primitive family of extant ferns is characterized by macroscopic sporangia whose walls are many cell layers thick. Fronds with sterile and fertile portions, the fertile developing on a stipe that arises below the sterile blade.

1. Blades entire, reticulately veined, margins entire; fertile spike unbranched, sporangia embedded in compact linear spike ...................................................... 1. *Ophioglossum*

2. Blades pinnately divided or lobed, veins free, margins entire to dentate; sporangia sessile or terminating short stalks ........................................ 2. *Botrychium*

1. *Ophioglossum* Linnaeus

   Adder’s-tongue

   Sterile portion of fronds entire, ovate to lanceolate, venation reticulate; fertile portions of fronds simple with sporangia in two rows.

1. Stems globose; frond ≤1 cm long, blade deltoid .................................. 1. *O. crotalophoroides*

2. Stem elongate; frond >1 cm long, blade ovate to lanceolate....................2

   2. Sporangial cluster 0.5-1.5 cm long with 5-12 sporangia pairs............. 2. *O. nudicaule*

   2. Sporangial cluster 2-4 cm long with 12-40 sporangia pairs.............. 3

3. Sterile leaves with veins forming small aeroles within larger aeroles.. 3. *O. engelmannii*

3. Sterile leaves with veins only branched or nonbranched within large aeroles, but not forming smaller aeroles ........................................ 4. *O. petiolatum*
1. *O. crotalophoroides* Walter - BULBOUS ADDER’S TONGUE FERN. Figure 8e, 8f. Grassy areas including lawns, roadside clearings and cemeteries.

2. *O. nudicaule* Linnaeus - DWARF ADDER’S TONGUE FERN. Figure 9a, 9b. Sandy, moist habitats such as grassy areas and cemeteries.

3. *O. engelmannii* Prantl - LIMESTONE ADDER’S TONGUE FERN. Figure 9c, 9d. Limestone derived soils of the Black Belt and limestone outcrops.

4. *O. petiolatum* Hooker – STALKED ADDER’S TONGUE. Figure 9e, 9f. Grassy areas including lawns. Introduced.

2. BOTRYCHIUM Swartz

Grapefern

Roots fleshy; blades 2.5-40.0 cm long, broadly triangular, bipinnate to tripinnate; fertile stalk arising from base of blade or base of petiole; sporangia on branching segments at upper end of fertile stalk.

1. Vegetative leaves with open sheaths; fertile stalks arising from the base of the blades of vegetative leaves ..............................................................1. *B. virginianum*

1. Vegetative leaves with closed sheaths; fertile stalks arising near ground level from basal portion of petioles of vegetative leaves ..............................................................2

2. Vegetative leaves prostrate, blades two per plant; roots yellowish...2. *B. lunarioides*

2. Vegetative leaves erect or ascending, blades one per plant; roots black ...3

3. Basal pinnae alternate ............................................................................. 3. *B. jenmanii*

3. Basal pinnae opposite to subopposite ..................................................4

4. Pinnules sharply serrate, lateral lobes oblong and somewhat rounded; blades remaining green in winter ........................................4. *B. bitemnotum*

4. Pinnules entire or lobed, lateral lobes lanceolate; blades turning bronze in winter .................................................................5. *B. dissectum*

1. *B. virginianum* (Linnaeus) Swartz - RATTLESNAKE FERN. Figure 10c, 10d. Moist deciduous woodlands in well drained soils.

2. *B. lunarioides* (Michaux) Swartz - WINTER GRAPEFERN. Figure 10a, 10b. Cemeteries; rare on sandy roadsides or pastures.

3. *B. jenmanii* L. Underwood - ALABAMA GRAPEFERN. Figure 10e, 10f. Both xeric woodlands and mesic wooded ravines.

4. *B. bitemnotum* (Savigny) L. Underwood - SOUTHERN GRAPEFERN. Figure 11a, 11b. Moist woodlands along stream banks and old fields.

5. *B. dissectum* Sprengel - DISSECTED GRAPEFERN. Figure 11c, 11d. Moist mesic woodlands along streambanks and mesic open areas

10. OSMUNDACEAE Berchtold & J. Presl

OSMUNDA Linnaeus

Royal Fern

Roots black, wiry; fronds pinnate-pinnatifid to bipinnate; rachis grooved; pinnae monomorphic or dimorphic; sori absent; sporangia on modified fertile segments of blades or separate fronds.

1. Fertile and sterile leaves on separate petioles, sterile leaves pinnate-pinnatifid; tufts of hairs persistent on abaxial surface of pinnae near base ....................1. *O. cinnamomea*

2. Fertile and sterile leaves on same petiole, sterile leaves bipinnate; tufts of hairs absent on abaxial surface of pinnae near base .................................2. *O. regalis*

1. *O. cinnamomea* Linnaeus - CINNAMON FERN. Figure 11e, 11f. In swamps, wet woods and along stream banks.

2. *O. regalis* Linnaeus - Our’s is represented by *O. regalis* var. *spectabilis* (Willdenow) A. Gray - ROYAL FERN. Figure 12a, 12b. In swamps, wet woods and along stream banks.

11. DENNSTAEDTIACEAE Chling

PTERIDIUM Gleditsch ex Scopoli, Bracken Fern

Rhizomes long, creeping; fronds 45-90 cm long; blades broadly triangular, bipinnate-pinnatifid to tripinnate; sori linear, marginal, covered by reflexed margin of blade.

1. *P. aquilinum* (Linnaeus) Kuhn – Figure 12c, 12d. Two varieties of *P. aquilinum* grow in South Alabama. *Pteridium aquilinum* var. *latusculum* (Desvaux) L. Underwood ex A. Heller - EASTERN BRACKEN. Terminal segment of pinnules <4x as long as wide; pinnae pubescent beneath. Wooded slopes and dry open areas, in full to partial sun. *Pteridium aquilinum* var. *pseudocaudatum* (Clute) A. Heller - TAILED BRACKEN. Terminal segment of pinnules >4x as long as wide; pinnae glabrescent beneath. Wooded slopes and dry open areas, in full to partial sun.

12. PTERIDACEAE Reichenbach

Rhizomes creeping, branched; petiole with 1-3 adaxial grooves; terminal segment of blade sessile to short-stalked; sori under reflexed margins of pinnules.

1. Sori separate along pinnae margins; leaves bright green, delicate ..........1. *Adiantum*

2. Sori continuous along pinnae margins or concentrated on small apical and lateral lobes; leaves dark-green, tough .........................................................2

2. Petiole rounded adaxially; sori concentrated on small apical or lateral lobes ..................................................................................2. Cheilanthes

3. Petiole with 2-3 grooves adaxially; sori continuous along pinnae margins.3. *Pteris*

1. ADIANTUM Linnaeus
Maidenhair Fern

Rhizomes creeping; fronds 25-65 cm long; petioles shiny, dark brown to black; blades 15-35 cm long, fan-shaped to lanceolate; sori oblong under reflected margins of pinnules.

1. Blades fan-shaped; pinnules oblong, 3x longer than wide ....................1. A. pedatum
2. Blades lanceolate; pinnules rhomboid, cuneate, as long as wide 2. A. capillus-veneris

1. A. pedatum Linnaeus - NORTHERN MAIDENHAIR FERN. Figure 12e, 12f. Rich mesic hardwood slopes.
2. A. capillus-veneris Linnaeus - SOUTHERN MAIDENHAIR FERN. Figure 13a, 13b. Wet crevices of limestone on riverbanks.

2. CHEILANTHES Swartz

Lip Fern

Rhizomes compact to short-creeping, ascending to horizontal; fronds 7-70 cm long; petiole dark brown; blades 1.5-5.0 cm wide, linear-oblong to lanceolate; sori concentrated on small apical and lateral lobes.

1. C. lanosa (Michaux) D.C. Eaton – HAIRY LIP FERN. Figure 13c, 13d. Rocky slopes and ledges.

3. PTERIS Linnaeus

Brake Fern

Rhizomes short, creeping; fronds 25-60 cm long; petioles 10-20 cm long, smooth; blades 15-40 cm long, oblong-triangular, pinnate; rachis winged; sori submarginal under reflected margins of blade.

1. Fronds 1-pinnate, pinnae entire to divided; petioles shorter than rachis, scales present.................................................................1. P. vittata
2. Fronds partly bi-pinnate, some pinnule lobed or divided; petioles longer than rachis, scales absent .................................................................2
3. Fronds divided into 4-6 pinnule pairs; rachis winged 2. P. multifida
4. Fronds divided into 1-3 pinnule pairs; rachis not winged 3. P. cretica

1. P. vittata Linnaeus – LADDER FERN. Figure 13e, 13f. Roadsides and various habitats. Introduced.
2. P. multifida Poiret – SPIDER BRAKE. Figure 14a, 14b. Damp soil and rocks. Oftentimes found growing on old rock and brick walls in shady areas. Introduced.
3. P. cretica Linnaeus – Figure 14c, 14d. Two varieties of P. cretica grow in South Alabama. P. cretica var. cretica – CRETAN BRAKE. Pinnae green throughout. On rocks, woods slopes, river banks. Pteris cretica var. albolineata Hooker - WHITE-LINED CRETAN BRAKE. Pinnae with white, central stripe. On rocks, woods slopes, river banks. Both are introduced.

13. THELYPTERIDACEAE Ching ex Pichi-Sermolli

Rhizome long, creeping; fronds pinnate-pinnatifid to bipinnate; blades oblong to triangular; sori round to oblong, medial to submarginal; indusia kidney-shaped or absent.

1. Leaves 1-pinnate; indusia diameter >0.3 mm ........................................1. Thelypteris
   2. Indusium absent; stem diameter 1-4 mm; rachis winged throughout 2. Phegopteris
   3. Indusium present; stem diameter 8-10 mm; rachis not winged or winged at apical portion of blades only........................................................3. Macrothelypteris

1. Thelypteris Schmidel

Marsh Fern

Rhizome long, creeping; fronds 40-110 cm long; blade 20-75 cm long, lanceolate to ovate-lanceolate, pinnate-pinnatifid; sori round, medial to submarginal.

1. Petioles green with dark bases; stems diameter <4mm .........................1. T. palustris
2. Petioles brown to purple; stems diameter >4.1 mm ................................2
3. Some basal veins of pinnules united below sinuses; petioles purplish brown ...2. T. dentata
4. Some basal veins of pinnules free or extending to sinuses; petioles straw colored...3
5. Midrib on adaxial leaf surface glabrous or with few trichomes <0.2mm long; plants growing on limestone .................................................................3. T. ovata

6. Midrib on adaxial leaf surface pubescent; plants growing in various soils..............4
7. Sori medial; basal 1-2 pairs of pinnae not reduced; adaxial secondary veins of pinnae glabrous or with few trichomes........................................4. T. kunthii
8. Sori submarginal; basal 1-2 pairs of pinnae reduced; adaxial secondary veins of pinnae pubescent.................................................................5. T. hispidula

1. T. palustris Schott - MARSH FERN. Figure 14e, 14f. Wet swampy woods and open areas.
2. T. dentata (Forsskål) E. P. St. John - DOWNY MAIDEN FERN. Figure 15a, 15b. Mesic woods, pastures and roadsides. Introduced.
3. T. ovata R. P. St. John - OVATE MAIDEN FERN. Figure 15c, 15d. Limestone banks of rivers.
4. T. kunthii (Desvaux) C. V. Morton - SOUTHERN SHIELD FERN. Figure 15e, 15f. Wet soil in swampy woods, stream banks and rock crevices.
5. T. hispidula (Descaisne) C. F. Reed - Ours is represented by T. hispidula var. versicolor
Pteridophytes of Southeast Alabama

1. Leaves monomorphic; sterile blades once-pinnate to pinnatifid to pinnate-pinnatifid, ovate-deltoid to ovate-triangular; sori oblong in chain-like rows.

2. PHEGOPTERIS (C. Presl) Fée
   Beech Fern
   Rhizomes long, creeping; fronds 35-70 cm long; blades 15-30 cm long, broadly triangular, long pointed apex, pinnate-pinnatifid; sori round, marginal; indusium lacking.

1. P. hexagonoptera (Michaux) Fée - BROAD BEECH FERN. Figure 16c, 16d. Mesic woodlands and rich ravines.

3. MACROTHERYPTERIS (H. Itô) Ching
   Rhizomes long, creeping; fronds 60-125 cm long; blades 35-70 cm long, broadly triangular, bipinnate-pinnatifid; rachis winged toward apex; sori round, sub-marginal; indusium short-lived.

1. M. torresiana (Gaudichaud-Beaupré) Ching - MARIANA MAIDEN FERN. Figure 16e, 16f. Along stream banks and other wet areas. Introduced.

14. POLYPODIACEAE Berchtold & J. Presl
   PLEOPELTIS Humboldt & Bonpland ex Willdenow
   Golden Polypodies
   Rhizomes long, creeping, slender; fronds 5-18 cm long, deeply pinnatifid; blades oblong, 3-10 cm long, abaxial surface silvery brown with scales; sori round, marginal, naked.

1. P. polypodioides (Linnaeus) E. G. Andrews & Windham – Ours is represented by P. polypodioides var. michauxiana (Weatherby) E. G. Andrews & Windham - RESURRECTION FERN. Figure 17a, 17b. Epiphytic on trunks and branches of trees with a rough periderm, can form dense mats on clay soil of road cuts.

15. BLECHNACEAE C. Presl
   WOODWARDIA Smith
   Chain Fern
   Rhizomes long, creeping; fronds 30-130 cm long, monomorphic or dimorphic; blades pinnatifid to pinnate-pinnatifid, ovate-deltoid to ovate-triangular; sori oblong in chain-like rows.

1. Leaves monomorphic; sterile blades once-pinnate.........................1. W. virginica
1. Leaves dimorphic; sterile blades pinnatifid...............................2. W. areolata
1. W. virginica (Linnaeus) Smith - VIRGINIA CHAIN FERN. Figure 17c, 17d. Swampy woods and roadside ditches.

2. W. areolata (Linnaeus) T. Moore - NETTED CHAIN FERN. Figure 17e, 17f. Swamps and stream banks.

16. ASPLENIACEAE Newman
   ASPLENIUM Linnaeus
   Spleenwort
   Rhizomes short, thick; fronds 5-40 cm long, monomorphic; rachis brown to black; blades pinnate, oblong; sori elongate, medial to sub-marginal; indusium laterally attached.

1. Pinnae 1.5-2.5 mm long, alternate, sessile; auricle of pinnae overlapping rachis; rachis black .................................................................2. A. platyneuron
2. Pinnae 0.5-1.4 mm long, opposite, short petiolules; auricle of pinnae not overlapping rachis; rachis dark brown...................................................3. A. resiliens

1. A. platyneuron (Linnaeus) Britton, Sterns, & Poggenburg - EBONY SPLEENWORT. Figure 18a, 18b. Mesic woods, xeric woods and old fields.
2. A. resiliens Kunze - BLACK-STEMMED SPLEENWORT. Figure 18c, 18d. Crevices of limestone rocks in deep shaded areas.

17. DRYOPTERIDACEAE Herter
   Rhizomes long, creeping; fronds monomorphic or dimorphic; blades pinnatifid to bipinnate; sori mostly abaxial, medial to marginal; sporangia stalked; spores oblong or reniform.

1. Sporangia on separate stalks from vegetative leaves.................................1. Onoclea
2. Indusia completely surrounding receptacle; petiole with 2 vascular bundles...2. Woodsia
3. Fronds pinnate ...........................................................................4
4. Fronds with <13 pairs of pinnae, pinnae serrate with well developed basal auricle; sori completely covering abaxial surface of pinnae ..........3. Polystichum
5. Fronds with >13 pairs of pinnae, pinnae undulate or dentate without a basal auricle; sori not completely covering abaxial surface of pinnae ....4. Cyrtomium
6. Sori elongated; petioles with 2 vascular bundles..................................6
7. Sori round; petioles with >3 vascular bundles......................................7
8. Petioles yellowish green to reddish, glabrous or with a few scattered, chaffy scales; multicellular hairs absent on costa.................................5. Athyrium
9. Petioles light brown with long brown scales; multicellular hairs borne along costae .........................................................6. Deparia
10. Indusia absent; petioles with scattered scales at base...........................7. Dryopteris
7. Indusia present; petioles densely scaly throughout ......................... 3. Polystichum

1. ONOCLEA Linnaeus  
Sensitive fern

Rhizomes long, slender, creeping, green; fronds dimorphic, sterile 30-80 cm long, fertile 20-40 cm long; blades 15-40 cm long, pinnatifid into 12 pairs of oblong segments; sori in segmented segments at end of fertile stalks.

1. O. sensibilis Linnaeus - SENSITIVE FERN. Figure 18e, 18f. Swampy woodlands, roadside ditches.

2. WOODSIA R. Brown  
Cliff fern

Rhizomes short, creeping; fronds 20-55 cm long; blades oblong, 10-30 cm long, pinnate-pinnatifid; sori round, marginal; indusia splitting along several sutures.

1. W. obtusa (Sprengel) Torrey - BLUNT-LOBED CLIFF FERN. Figure 19a, 19b. Xeric, often sunny roadside banks.

3. POLYSTICHUM Roth  
Christmas fern

Rhizomes long, creeping; fronds 25-75 cm long, evergreen; petioles with tan scales; blades oblong-lanceolate, 20-55 cm long, pinnae auriculate; fertile pinnae upper one-half of frond; sori round, submedial; indusia peltate.

1. Fronds 1 pinnate, fertile and sterile pinnae dimorphic ............... 1. P. acrostichoides
2. Fronds bipinnate, fertile pinnae and sterile pinnae isomorphic .............. 2. P. braunii

1. P. acrostichoides (Michaux) Schott - CHRISTMAS FERN. Figure 19c, 19d. Shaded, mesic woods, ravines and creek banks.
2. P. braunii (Spener) Fée – BRAUN’S HOLLY FERN. Figure 19e, 19f. Moist soils in mixed pines and hardwoods. Introduced.

3. CYRTOMIUM C. Presl  
Holly fern

Rhizomes short, covered with brown scales; fronds 25-50 cm long; blades pinnate, 15-40 cm long, oblong-ovate; pinnae 4-10 pairs, alternate; sori round, scattered; indusia peltate.

1. C. falcatum (Linnaeus f.) C. Presl - ASIATIC HOLLY FERN. Figure 20a, 20b. Mesic ravines. Introduced.

5. ATHYRIUM Roth  
Lady fern

Rhizomes short, creeping; fronds 25-130 cm long; rachis green or reddish; blades ovate or oblanceolate, 20-100 cm long, bipinnate or tripinnate; sori elongated, straight or curved, sub-marginal; indusia marginally ciliate.

1. A. filix-femina (Linnaeus) Roth ex Mertens. Ours is resented by A. filix-femina var. asplenioides (Michaux) Farwell - SOUTHERN LADY FERN. Figure 20c, 20d. Swampy woods, creek banks and roadside ditches.

6. DEPARIA Hooker & Greville

Rhizomes short, creeping; fronds 30-60 cm long; blades oblong-triangular, 15-35 cm long, pinnate-pinnatifid; pinnae oblong with long, tapering apices; sori elongated; indusia laterally attached.

1. D. petersenii (Kunze) M. Kato - PETERSONS TWIN-SORUS FERN. Figure 20e, 20f. Moist soils in disturbed areas and along stream banks. Introduced.

7. DRYOPTERIS Adanson  
Shield fern

Rhizomes creeping, covered with tan scales; fronds 60-130 cm long; blades pinnate-pinnatifid, 45-90 cm long, elliptic-lanceolate; sori round, medial; indusia peltate.

1. Fertile pinnae narrower than sterile, more widely spaced, restricted to the distal one-half of blade; scales at petiole base tan; fronds evergreen................ 1. D. ludoviciana
2. Fertile pinnae and sterile same size, equally spaced, occupying distal one-half of blade to entire blade; scales at petiole base brown; fronds deciduous .......... 2. D. celsa

1. D. ludoviciana (Kunze) Small - SOUTHERN SHIELD FERN. Figure 21a, 21b. Mesic woods and swamps. Often associated with limestone.
2. D. celsa (W. Palmer) Knowlton – LOG FERN. Figure 21c, 21d. Swamps, wet woods and drainage ditches.
3. D. x australis (Wherry) Small - HYBRID SHIELD FERN. This is a sterile hybrid of D. ludoviciana (Kunze) Small and D. celsa (W. Palmer) Knowlton. Swamps. Known in southeast Alabama from a single collection in Conecuh County. This hybrid typically grows large like D. ludoviciana. Sporangia have few spores which are of various sizes.
Figure 1. a) illustration of *Equisetum hyemale*, b) distribution of *E. hyemale*, c) illustration of *Isoetes flaccida* megaspore, d) distribution of *I. flaccida*, e) illustration of *I. valida* megaspore, f) distribution of *I. valida*.

On the distribution maps, specimens deposited at TROY are represented by circles • and specimens deposited at other institutions are represented by squares ■.

Figure 2. a) illustration of *Isoetes appalachiana* megaspore, b) distribution of *I. appalachiana*, c) illustration of *I. melanpoda* megaspore, d) distribution of *I. melanpoda*, e) illustration of *I. louisianensis* megaspore, f) distribution of *I. louisianensis*. 
Figure 3. a) illustration of Isoetes hyemalis megaspore, b) distribution of I. hyemalis, c) illustration of I. boomii megaspore, d) distribution of I. boomii, e) illustration of Marsilea minuta, f) distribution of M. minuta.

Figure 4. a) illustration of Azolla caroliniana, b) distribution of A. caroliniana, c) illustration of Salvinia minima, d) distribution of S. minima, e) illustration of Selaginella apoda, f) distribution of S. apoda.
Figure 5. a) illustration of *Selaginella ludoviciana*, b) distribution of *S. ludoviciana*, c) *Lycopodium digitatum*, d) distribution of *L. digitatum*, e) illustration of *Lycopodiella cernua*, f) distribution of *L. cernua*.

Figure 6. a) illustration of *Lycopodiella caroliniana*, b) distribution of *L. caroliniana*, c) illustration of *L. appressa*, d) distribution of *L. appressa*, e) illustration of *L. x brucei* (shows angles of microphyll from erect stems), f) distribution of *L. x brucei*.
Figure 7. a) illustration of *Lycopodiella prostrata*, b) distribution of *L. prostrata*, c) illustration of *L. alopecuroides*, d) distribution of *L. alopecuroides*, e) illustration of *L. x copelandii* (shows angles of microphylls from erect stems), f) distribution of *L. x copelandii*.

Figure 8. a) illustration of *Lycopodiella alopecuroides x prostrata* (shows angles of microphylls from erect stems), b) distribution of *Lycopodiella alopecuroides x prostrata*, c) illustration of *Lygodium japonicum*, d) distribution of *L. japonicum*, e) illustration of *Ophioglossum crotalophoroides*, f) distribution of *O. crotalophoroides*. 

222 223
Figure 9. a) illustration of *Ophioglossum nudicaule*, b) distribution of *O. nudicaule*, c) illustration of *O. engelmannii*, d) distribution of *O. engelmannii*, e) illustration of *O. petiolatum*, f) distribution of *O. petiolatum*.

Figure 10. a) illustration of *Botrychium lunarioides*, b) distribution of *B. lunarioides*, c) illustration of *B. virginianum*, d) distribution of *B. virginianum*, e) illustration of *B. jenmanii*, f) distribution of *B. jenmanii*. 
Figure 11.  a) illustration of *Botrychium biternatum*, b) distribution of *B. biternatum*, c) illustration of *B. dissectum*, d) distribution of *B. dissectum*, e) illustration of *Osmunda cinnamomea*, f) distribution of *O. cinnamomea*.

Figure 12.  a) illustration of *Osmunda regalis*, b) distribution of *O. regalis*, c) illustration of *Pteridium aquilinum*, d) distribution of *P. aquilinum*, e) illustration of *Adiantum pedatum*, f) distribution of *A. pedatum*.
Figure 13. a) illustration of *Adiantum capillus-veneris*, b) distribution of *A. capillus-veneris*, c) illustration of *Cheilanthes lanosa*, d) distribution of *C. lanosa*, e) illustration of *Pteris vittata*, f) distribution of *P. vittata*.

Figure 14. a) illustration of *Pteris multifida*, b) distribution of *P. multifida*, c) illustration of *P. cretica*, d) distribution of *P. cretica*, e) illustration of *Thelypteris palustris*, f) distribution of *T. palustris*. 
Figure 15. a) illustration of *Thelypteris dendata*, b) distribution of *T. dendata*, c) illustration of *T. ovata*, d) distribution of *T. ovata*, e) illustration of *T. kunthii*, f) distribution of *T. kunthii*.

Figure 16. a) illustration of *Thelypteris hispidula*, b) distribution of *T. hispidula*, c) illustration of *Phegopteris hexagonoptera*, d) distribution of *P. hexagonoptera*, e) illustration of *Macrothelypteris torresiana*, f) distribution of *M. torresiana*. 
Figure 17. a) illustration of *Pleopeltis polypodioides*, b) distribution of *P. polypodioides*, c) illustration of *Woodwardia virginica*, d) distribution of *W. virginica*, e) illustration of *W. areolata*, f) distribution of *W. areolata*.

Figure 18. a) illustration of *Asplenium platyneuron*, b) distribution of *A. platyneuron*, c) illustration of *A. resiliens*, d) distribution of *A. resiliens*, e) illustration of *Onoclea sensibilis*, f) distribution of *O. sensibilis*.
Figure 19.  a) illustration of *Woodsia obtusa*, b) distribution of *W. obtusa*, c) illustration of *Polystichum acrostichoides*, d) distribution of *P. acrostichoides*, e) illustration of *P. braunii*, f) distribution of *P. braunii*.

Figure 20.  a) illustration of *Cyrtomium falcatum*, b) distribution of *C. falcatum*, c) illustration of *Athyrium filix-femina*, d) distribution of *A. filix-femina*, e) illustration of *Deparia petersenii*, f) distribution of *D. petersenii*.
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BOOK REVIEW

HUMAN PERFECTION THROUGH BIOTECHNOLOGY: SHOULD WE GO FOR IT?

Drew Humphries* and James T. Bradley
Department of Biological Sciences, Auburn University
Auburn, AL 36849
Correspondence: James T. Bradley (bradljt@auburn.edu)


Humans have long mystified, sanctified, or otherwise placed special significance on their own reproductive process. Evidence for this ranges from 28,000-year-old Venus figurines of the Gravettian culture celebrating female fertility to in vitro fertilization (IVF) clinics and the high technology neonatal units of modern hospitals. Birth and first breath mark our entry into the world of opposites – good and evil, truth and falsehood, peace and violence. Not many years after taking our first breath, which some religious traditions mark as the moment of ensoulment, we develop into agents of choice – autonomous creatures making moral decisions about our own lives and our interactions with others. Now modern genetic and reproductive biotechnologies including gene therapy, genetic enhancement, and assisted reproduction technologies present us with new moral decisions associated with procreation itself. In The Case against Perfection, an expansion of an essay by the same title published in The Atlantic in 2004, Harvard political philosopher/ethicist Michael Sandel argues against attempts to “perfect” humanity through genetic enhancement, while supporting the future use of gene therapy and embryonic stem cell technology to relieve human suffering. This position presumes that one can clearly distinguish between enhancement and therapy, a feat that no bioethicist has yet successfully accomplished; nevertheless, Sandel forges ahead to explain why he believes that using biotechnologies to enhance human physical and cognitive characters beyond normality toward “perfection” will ultimately desanctify human procreation.

What knowledge and technologies are so powerful as to bring up the notion of human “perfectability?” Completion of the Human Genome Project in the early years of this century revealed humans to be constructed from the products of about 25,000 genes. The Online Mendelian Inheritance in Man (OMIM) site lists the complete base sequences and chromosomal locations for over 12,000 of these whose inheritance is easily predictable. Specific disease and nondisease traits are known for almost 400 of these genes, and once a disease-causing allele is identified it can be detected using the DNA from a single cell removed from an 8-cell embryo created by IVF. Single-cell embryo biopsy to detect disease-causing genes or chromosomal abnormalities is called pre-implantation genetic diagnosis (PGD). Since 1989 PGD has been used to detect embryos bearing disease-causing chromosomal abnormalities and to allow for the selection of genetically healthy embryos for transfer to the womb. The possibility now exists to test a pre-implantation embryo for any one of the 12,000 genes (and their variants) listed on the OMIM site. Moreover, within a decade it is likely that human geneticians will link hundreds (perhaps thousands) of these with non-disease physical and personality traits ranging from stature to shyness. Such functional genomic information, coupled with IVF, PGD, and the approaching ability to introduce modified or designed genes into the human germline will give humankind the power to direct its future evolution toward its own concept of perfection. This power is what troubles Michael Sandel.

In the first of five chapters, Sandel argues convincingly that traditional arguments against (or for) realizing the prospect of genetically enhancing cognitive and physical human traits such as athletic prowess, stature, musical ability and memory do not cut to the core of the morality of such enhancements. Traditional arguments against human genetic enhancement include (1) that parentally designed genetic enhancement of unborn children, particularly germ line enhancements apt to remain in the descendants of those children, violate the autonomy of the unborn, (2) that genetic enhancements in some would be unfair to others attempting to compete on the same “playing field,” and (3) that distributive justice in the availability of such enhancements would not be possible. Traditional arguments for moving ahead to develop technologies of human genetic enhancement usually invoke the importance of protecting individual rights. According to Sandel, all of these arguments miss the mark because they do not focus on the rightness or wrongness of aspiring to enhancement itself. Sandel writes that “to grapple with the ethics of enhancement, we need to confront questions largely lost from view in the modern world – questions about the moral status of nature, and about the proper stance of human beings toward the given world” (p. 9). Sandel addresses these questions in the final chapter of the book after discussing examples of what he believes would be inappropriate human interventions into nature: the genetic enhancement of athletic prowess and the genetic selection/design of children.

For Sandel, what is fundamentally wrong with drug or genetically enhanced performance in athletes, or even musicians, goes deeper than breaking rules or risking one’s health. “The real problem with genetically altered athletes,” Sandel writes, “is that they corrupt athletic competition as a human activity that honors the cultivation and display of natural talents” (p. 29).

For similar reasons, he argues against the current use of PGD by some parents to select the gender of their children, and against future use of the technology to select for traits that have no medical significance.

Currently PGD is used primarily to screen preimplantation embryos for potential genetic disabilities. The world is not perfect, and sometimes our intervention seems appropriate. How could anyone find it objectionable to use PGD to prevent a child from...
being born with some horrible disease or disability? But herein lies a debate over ambiguity: namely, how one ought to distinguish between what is normal and abnormal, between what interventions count as therapy and which ones constitute enhancement. There are conditions that may be considered debilitating by some but valued by others. To illustrate, Sandel cites the instance of a deaf, lesbian couple which desires to give birth to a deaf child. In choosing a sperm donor who had a family history of deafness, the couple succeeded in giving birth to a deaf son. Public criticism immediately followed the birth, proclaiming that the couple had deliberately and unethically disabled their child. The couple argued that they viewed deafness as a “cultural identity” that they were proud of, and wanted their child to share in this identity with them.

Down syndrome presents a similar study in ambiguity. PGD allows detection of Down syndrome embryos prior to pregnancy, but more commonly Down syndrome is diagnosed during the first trimester by chorionic villus sampling or during the second trimester by amniocentesis. Parents whose fetus is diagnosed with Down syndrome must then decide whether to terminate the pregnancy. Is it right to abort a fetus or reject an embryo with trisomy in chromosome 21? Given the learning and motor skills disabilities that accompany this condition, some people think it is best to actively prevent the birth of a Down syndrome child; however, others point to the joys of having a child with special needs in the family and cite the loving and joyful characteristics of many Down syndrome persons as natural gifts. Should societal consensus, individual parents’ values, physicians’ values, or biology dictate what is “normal” or what constitutes a “gift”? Clearly, answers to questions like these will reflect the cultural, religious, and experiential diversity of our pluralistic society and of the global village itself.

Beyond therapy and the gray areas between therapy and enhancement and “normal” and “abnormal” lies the realm of enhancement via genetic engineering and/or PGD for nonmedical purposes such as height, musculature, skin color, cognitive characters like memory, personality traits, and perhaps even propensities for abilities in mathematics, music, art, etc. Enhancement proponents point out human genetic enhancement would not differ qualitatively from what many parents already do to influence the development of their children or to give them advantages in life, i.e. music/sports lessons, summer science camps, college educations. Sandel acknowledges that good parents take responsibility for the welfare of their children; however, he views the “heavily managed, high pressure child-rearing practices” of hyperparenting, and the bioengineering of children to be similar in spirit and equally undesirable (pp. 61-62). Both are manifestations of human hubris. Even if motivated by society’s competitive demands, hyperparenting and genetic enhancement represent “an anxious excess of mastery and domination that misses the sense of life as gift” and are disturbingly reminiscent of past eugenics programs (pp 61-62).

Forced sterilization of over 60,000 genetically “deficient” Americans in the early 20th century and the horrors of Nazi death camps are extreme examples of the old eugenics. Today “an influential school of Anglo-American political philosophers” promote a so-called liberal eugenics (p 75). In this new version of eugenics, the only requirement is that whatever human genetic engineering is to be performed must not violate the autonomy of the person at whom it is directed. Though neither an embryo nor a child can be autonomous, it is essential that any care provided by the parents must not willingly influence the future plans of that child or embryo. While liberal eugenics attempts to justify genetic enhancement by protecting the future decisions of those affected (e.g. via reversible genetic engineering), Sandel argues that it still represents “a stance of mastery and domination that fails to appreciate the gifted character of human powers and achievements, and misses the part of freedom that consists in a persisting negotiation with the given” (p 83).

The ethical theme running throughout the book is that humans ought to appreciate and respect the giftedness of life. By “gifts,” Sandel means talents or conditions that are bestowed upon us: “the talent in question is not wholly the athlete’s or the musician’s own doing; whether he has nature, fortune, or God to thank for it, the talent is an endowment that exceeds his control” (p. 93). Sandel denies that belief in a supernatural Gift-Giver is required to view the genetic hand dealt by life as a gift. We can just as well thank nature or chance for our biological gifts. Without this idea of giftedness, Sandel believes that “three key features of our moral landscape – humility, responsibility, and solidarity” (p. 86) - would be transformed for the worse and would “leave us with nothing to affirm or behold outside our own will” (p. 100). In response to those who view bioengineering as an exercise in human freedom, Sandel writes that “changing our nature to fit the world, rather than the other way around, is actually the deepest form of disempowerment” (p. 97).

So what about persons who are disempowered due to their genetic lot in life? Sandel believes one can draw a clear distinction between healing and enhancing. He acknowledges that the goal of medicine is to restore normal human functioning, and that it therefore does not represent an attempt to master our surroundings. Medicine does intervene in nature, and Sandel is not bothered by this, stating that, “Not everything is good. Smallpox and malaria are not gifts, and it would be good to eradicate them” (p 101). For the same reason, Sandel favors human embryonic stem cell (ESC) research and use if it is directed toward relieving suffering caused by disease or injury, but he opposes ESC research aimed at human enhancement. Use of human embryos for ESC therapy does not bother Sandel. He believes that human embryos deserve respect for their potential to develop into persons but that they do not have the moral status of newborns.

In our view, one weakness in Sandel’s argument is his failure to acknowledge and deal with the great difficulty in distinguishing between enhancement of the normal and therapy for the abnormal. When “normality” is viewed largely as a social construct, a subjective valuation of traits such as height, amount of body fat, or even cognitive talents that may vary between groups and through time, the line between gene therapy and genetic enhancement also becomes dependent on place and time. Some authors have creatively addressed the therapy/enhancement difficulty, and Sandel would have done well to discuss their ideas. For example, Erik Parens suggests adding to treatment and enhancement a third category, prevention, in order to help determine what interventions ought to be covered by health insurers or be considered proper goals of medicine. Parens notes that enhancement of the immune system via vaccinations belongs in the “prevention” category and is a proper goal of medicine. Secondly, we are uncomfortable with Sandel’s notion that “negotiation with the given” is morally superior to using our knowledge of nature for self-improvement. Would Sandel take a similar stance within the agricultural domain and maintain that it is morally preferable to negotiate with the “given” of weeds and insect pests rather than to develop herbicide-resistant beans and insect resistant corn through genetic engineering?
Or what if we someday have the power to divert hurricanes away from highly populated areas? Would negotiating what nature throws at us by evacuating and boarding up windows be superior to exercising that power? But perhaps Sandel is only concerned about the enhancement of human traits and not with the engineering of plant traits or weather events; if so, he ought to say so and explain why he singles out humanity as the one component of nature in which science-based improvements should be constrained.

In summary, Sandel’s book is clearly written, scientific and ethical concepts are explained with a general audience in mind, and a new argument (“giftedness”) is offered to the debate about how modern biotechnologies ought to be used. Whether one is for or against human genetic enhancement, a close reading of The Case Against Perfection will give important information and a fresh perspective on the issue.

*Drew Humphries is a recent graduate in Zoology at Auburn University. This review was written for a senior level Bioethics Research course with mentoring and editing by James T. Bradley, Department of Biological Sciences, 331 Funchess Hall, Auburn, AL 36849.

2 The total number of genes in the human genome is still contested, but recent estimates range between 20,000 and 30,000 as reported on the official website of the Human Genome Project: http://www.ornl.gov/sci/techresources/Human_Genome/faq/generumber.shtml

Authors Index

Adinarayana, Andukuri .............................................................................................................................. 120
Aggarwal, M ................................................................................................................................... 139
Allen, Bryant K ............................................................................................................................... 134
Allison, Brittany M ............................................................................................................................ 137
Amsler, Charles D ............................................................................................................................. 80, 89
Amsler, Margaret O ............................................................................................................................. 89
Anderson, Joel M ................................................................................................................................... 80
Angela Smith ........................................................................................................................................ 83, 84
Angus, Robert ...................................................................................................................................... 79, 100
Baker, Bill J ........................................................................................................................................ 89
Baldwin, Debra .................................................................................................................................... 25
Ballestas, Mary .................................................................................................................................... 94
Ballinger, Jared ..................................................................................................................................... 139
Bates, Larry W ..................................................................................................................................... 65
Batra, A. K ............................................................................................................................................ 135, 139
Beard, J. A ........................................................................................................................................... 97
Beard, Jordan A .................................................................................................................................. 89
Beck, P ............................................................................................................................................... 99
Bej, Asim K ......................................................................................................................................... 71, 74, 85
Bells, Susan L ...................................................................................................................................... 120
Benjamin, Ronald ............................................................................................................................... 135
Bentley, Keith ...................................................................................................................................... 110
Benveniste, Eddy N ............................................................................................................................ 89
Bhat, Kamala ....................................................................................................................................... 140
Bhatnagar, Vin ..................................................................................................................................... 137
Billington, Neil .................................................................................................................................... 75, 78, 81
Blakeney, Bryan A ............................................................................................................................... 120
Blankinship, Lisa Ann .......................................................................................................................... 88
Blough, Sean M .................................................................................................................................... 61
Boktazian-Johnson, Samantha S ........................................................................................................ 104
Booker, Haley ..................................................................................................................................... 114
Borden, Joel .......................................................................................................................................... 85
Boydstan, Jacob W ............................................................................................................................ 112
Boykin, D. Denise ............................................................................................................................... 105
Bradley, James T .................................................................................................................................. 70
Bradley, James ..................................................................................................................................... 144

242 243
<table>
<thead>
<tr>
<th>Name</th>
<th>Page(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bradley, Wayne</td>
<td>120</td>
</tr>
<tr>
<td>Branch, OraLee H</td>
<td>94</td>
</tr>
<tr>
<td>Breeden, Christina</td>
<td>61</td>
</tr>
<tr>
<td>Brice, Essence</td>
<td>108</td>
</tr>
<tr>
<td>Brooks, Sonja C</td>
<td>111</td>
</tr>
<tr>
<td>Brown, William S</td>
<td>105, 108, 110</td>
</tr>
<tr>
<td>Buckner, Ellen B</td>
<td>123, 124, 125, 127, 128</td>
</tr>
<tr>
<td>Burgess, J. Michael</td>
<td>142</td>
</tr>
<tr>
<td>Burgess, J.O.</td>
<td>92</td>
</tr>
<tr>
<td>Burgess, J.</td>
<td>98</td>
</tr>
<tr>
<td>Burnes, Brian</td>
<td>73, 80, 82, 103, 145</td>
</tr>
<tr>
<td>Busenlehner, Laura S</td>
<td>101</td>
</tr>
<tr>
<td>Bush, Gayle L</td>
<td>123</td>
</tr>
<tr>
<td>Byrd, Debra L</td>
<td>95</td>
</tr>
<tr>
<td>Cakir, D</td>
<td>92, 98, 99</td>
</tr>
<tr>
<td>Carrell, Holly</td>
<td>113</td>
</tr>
<tr>
<td>Carson, John D</td>
<td>97</td>
</tr>
<tr>
<td>Carter, Robert</td>
<td>72</td>
</tr>
<tr>
<td>Case, Jan</td>
<td>139</td>
</tr>
<tr>
<td>Casey, Ashley</td>
<td>112</td>
</tr>
<tr>
<td>Cassady, Carolyn J</td>
<td>104, 105, 110</td>
</tr>
<tr>
<td>Catrett, Jonathan</td>
<td>74</td>
</tr>
<tr>
<td>Cebrian, Just</td>
<td>95</td>
</tr>
<tr>
<td>Chapleau, Christopher</td>
<td>94</td>
</tr>
<tr>
<td>Chawla, K.K.</td>
<td>117</td>
</tr>
<tr>
<td>Chen, Yuan</td>
<td>110</td>
</tr>
<tr>
<td>Cheng, An-Jen</td>
<td>138</td>
</tr>
<tr>
<td>Chitrakar, Suman</td>
<td>75</td>
</tr>
<tr>
<td>Clark, Nancy</td>
<td>127</td>
</tr>
<tr>
<td>Cline, George</td>
<td>72, 91</td>
</tr>
<tr>
<td>Coleman, Andrew T</td>
<td>85</td>
</tr>
<tr>
<td>Collier, Linda A</td>
<td>95</td>
</tr>
<tr>
<td>Collin, Rachel</td>
<td>88</td>
</tr>
<tr>
<td>Cook, Todd</td>
<td>84</td>
</tr>
<tr>
<td>Cottier, John W</td>
<td>61, 62</td>
</tr>
<tr>
<td>Cox, Bryan D</td>
<td>109</td>
</tr>
<tr>
<td>Creech, Ronald E</td>
<td>78</td>
</tr>
<tr>
<td>Crutcher, Sihon</td>
<td>134</td>
</tr>
<tr>
<td>D’Abramo, Lou R</td>
<td>86</td>
</tr>
<tr>
<td>Daniel, Cameron H</td>
<td>134</td>
</tr>
<tr>
<td>Daniel, Nicholas H</td>
<td>144</td>
</tr>
<tr>
<td>Dashiff, Carol</td>
<td>129, 130</td>
</tr>
<tr>
<td>Davenport, L. J.</td>
<td>96, 97</td>
</tr>
<tr>
<td>Dean, D</td>
<td>92</td>
</tr>
<tr>
<td>Dean, Derrick D</td>
<td>120</td>
</tr>
<tr>
<td>DeAngelis, Tyson</td>
<td>75</td>
</tr>
<tr>
<td>DeLauney, Bryan</td>
<td>116</td>
</tr>
<tr>
<td>Dell’Italia, Louis</td>
<td>120</td>
</tr>
<tr>
<td>Denton, Tomas E</td>
<td>77</td>
</tr>
<tr>
<td>Diamond, Alvin</td>
<td>91, 199</td>
</tr>
<tr>
<td>Diaz, Maria Cristina</td>
<td>88</td>
</tr>
<tr>
<td>Dingler, Megan</td>
<td>112</td>
</tr>
<tr>
<td>Dobbins, E. G.</td>
<td>97</td>
</tr>
<tr>
<td>Dobbins, Elizabeth</td>
<td>97</td>
</tr>
<tr>
<td>Dokhanian, Mostafa</td>
<td>90</td>
</tr>
<tr>
<td>Dute, Roland</td>
<td>101</td>
</tr>
<tr>
<td>Edwards, Matthew</td>
<td>141</td>
</tr>
<tr>
<td>Elalaoui-Talibi, Hussain</td>
<td>140</td>
</tr>
<tr>
<td>Elfstrom, Gerard</td>
<td>69</td>
</tr>
<tr>
<td>Emily, Haanschoten</td>
<td>104</td>
</tr>
<tr>
<td>Enzor, Riki</td>
<td>83</td>
</tr>
<tr>
<td>Estes, Jennifer</td>
<td>145</td>
</tr>
<tr>
<td>Etting, Jessica E</td>
<td>76, 82</td>
</tr>
<tr>
<td>Ewell, Sharday</td>
<td>94</td>
</tr>
<tr>
<td>Fernandez, Karl</td>
<td>83, 84</td>
</tr>
<tr>
<td>Fogg, Ryan A</td>
<td>90</td>
</tr>
<tr>
<td>Fordham, Stephen</td>
<td>114</td>
</tr>
<tr>
<td>French, Kelly</td>
<td>62</td>
</tr>
<tr>
<td>Frings, David M</td>
<td>76, 101</td>
</tr>
<tr>
<td>Gaioso, Vanessa P</td>
<td>131, 132</td>
</tr>
<tr>
<td>Gangwar, Maulshree</td>
<td>71</td>
</tr>
<tr>
<td>Garner, Daphne O</td>
<td>65</td>
</tr>
<tr>
<td>Gaston, Janet L</td>
<td>78, 128, 144</td>
</tr>
<tr>
<td>Gauthier, Lynne</td>
<td>67, 68, 131</td>
</tr>
<tr>
<td>Ghuman, T</td>
<td>99</td>
</tr>
<tr>
<td>Gibbs, Victoria K</td>
<td>72</td>
</tr>
<tr>
<td>Gibson, Linda</td>
<td>125</td>
</tr>
<tr>
<td>Name</td>
<td>Page Numbers</td>
</tr>
<tr>
<td>-----------------------</td>
<td>--------------</td>
</tr>
<tr>
<td>Lott, Jill</td>
<td>112</td>
</tr>
<tr>
<td>Lopez, Linnet Busutil</td>
<td>88</td>
</tr>
<tr>
<td>LoCascio, Aaron C</td>
<td>137, 138</td>
</tr>
<tr>
<td>Lopez, Linnet Busutil</td>
<td>88</td>
</tr>
<tr>
<td>Lott, Jill</td>
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