Andrew C. Moore’s “Evolution Once More”: The Evolution-Creationism Controversy from an Early 1920s Perspective

Systematics and Biogeography of the *Notropis rubellus* Species Group (Teleostei: Cyprinidae)

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Andrew C. Moore's "Evolution One More": The Evolution-Creationism Controversy from an Early 1920s Perspective

by William D. Anderson, Jr.

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I asserted—and I repeat—that a man has no reason to be ashamed of having an ape for his grandfather. If there were an ancestor whom I should feel shame in recalling it would rather be a man—a man of restless and versatile intellect—who, not content with an equivocal success in his own sphere of activity, plunges into scientific questions with which he has no real acquaintance, only to obscure them by an aimless rhetoric, and distract the attention of his hearers from the real point at issue by eloquent digressions and skilled appeals to religious prejudice.

Thomas Henry Huxley
Andrew C. Moore’s “Evolution Once More”: The Evolution-Creationism Controversy from an Early 1920s Perspective

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ABSTRACT: Anderson, William D., Jr. 2002. Andrew C. Moore’s “Evolution Once More”: The Evolution-Creationism Controversy from an Early 1920s Perspective. Bulletin Alabama Museum of Natural History, Number 22: 1-35. Andrew Charles Moore, for many years Professor of Biology at the University of South Carolina, composed an essay on the dispute between evolutionists and creationists that was approaching the boiling point in the early 1920s. Apparently written in 1923, about two years before the famous Scopes Trial in Dayton, Tennessee, Moore’s views are remarkably modern and deserve to be disseminated widely. I present here Moore’s work, with an introduction, commentary, and annotations, and biographical materials on Moore, James Woodrow (scientist, educator, and theologian), who greatly influenced Moore, and their academic forebear Thomas Cooper (a many-talented genius), who pointed the way towards intellectual freedom.

Introduction
During a search for materials for a book on the history of natural history investigations in South Carolina (Sanders and Anderson, 1999), I discovered in the South Caroliniana Library, at the University of South Carolina in Columbia, an unpublished manuscript on the evolution-creationism controversy written by Andrew Charles Moore (1866-1928), a little-known biology professor at the University. Moore was particularly well suited to write about the controversy, being both an evolutionary biologist and a dedicated Christian layman. Apparently penned in 1923, about two years before the famous Scopes Trial in Dayton, Tennessee, and near the zenith of the antievolution movement that blossomed in the United States after the First World War, Moore’s analytical examination of the assertions made by the antievolutionists is as germane today as the day it was written. In an effort to place Moore’s composition in the context of the intellectual history of South Carolina, I present commentaries on Moore and on two of his predecessors in Columbia, Thomas Cooper (1759-1839) and James Woodrow (1828-1907).
Setting the Stage

Numbers and Stephens (1998: 59), in a cogent paper, have discussed the reception given Darwinism in the southern United States. While acknowledging that evolutionary thinking pervaded the South more slowly than the rest of the country, they maintained "that the South was far less uniform in its opposition to Darwinism than most scholarly accounts would suggest. In fact the very success of Darwinism in the South contributed significantly to the outburst of antievolutionism in the 1920s." One of the most telling observations made by Numbers and Stephens (1998: 67–68) was that no professor in the South, with the exception of James Woodrow (see below), appears to have lost a job over Darwinism before the First World War, despite the fact that evolutionary theory was taught frequently in both state and sectarian colleges. But things would not remain so calm after the War.

The relative tranquility evolutionists in the South enjoyed in the late nineteenth and early twentieth centuries declined rapidly in the years after World War I, when angry fundamentalists, convinced that the teaching of human evolution was causing many of the nation's social ills, tried to dislodge evolutionists from their professorships and to ban the offending doctrine in public schools (Numbers and Stephens, 1998: 73).

At the end of the First World War in 1918 the ultraconservative religious leaders, or Fundamentalists, had not yet focused nor even completely developed their antievolutionary fervor; in fact, they had no specific common objective except the "general defense of biblical orthodoxy within the church" (Larson, 1985: 41). The major factor that led to an environment conducive to the development of the virulent antievolutionary campaigns of the 1920s seems to have been the bitter opposition that had been developing over a period of years to the Higher Criticism of the Bible that was fostered by liberal theologians (Larson, 1985: 28–57; Numbers, 1992: 20–36).

In the 1920s there were a number of attempts to drive evolutionary biologists from Southern Baptist colleges; unfortunately, some of those efforts, including one in South Carolina, were successful. Andrew Lee Pickens (1890–1969), holder of degrees in both biology and theology, resigned in 1926 from the faculty of Furman University, a Baptist institution in Greenville, South Carolina, as a result of pressure that developed after a newspaper quoted him as endorsing evolutionary theory (Numbers, 1992: 48; Numbers and Stephens, 1998: 73). Pickens refused to recant when asked by the trustees of the institution "for his views on the evolution theory," declaring that he "had nothing to do but state them, which, of course, were in the affirmative and then resign. That is what I have done." He further maintained that "it is utterly foolish for a man to talk about teaching biology and not teaching evolution."

In states across the country legislators argued about the wisdom of antievolution laws, but only Tennessee, Mississippi, and Arkansas enacted legislation prohibiting the teaching of human evolution. Two other states demonstrated a lack of tolerance for the concepts of evolution; Oklahoma outlawed the use of textbooks dealing with evolution, and Florida "condemned the teaching of Darwinism as improper and subversive." The fact that all of the states forbidding the teaching of evolution were southern states, along with the wide attention given to the Scopes Trial in 1925, and the carnival atmosphere surrounding it, certainly contributed to the South's being considered by many as a stronghold of antievolutionism. Nevertheless, the vast majority of state legislatures in the South never prohibited the teaching of evolution in the 1920s (Numbers, 1992: 41; Numbers and Stephens, 1998:74). That the antievolutionism of the 1920s was not simply a regional phenomenon is well illustrated by the fact that "even the United States Senate debated—but eventually rejected—an amendment that would have banned radio broadcasts favorable to evolution" (Numbers, 1992: 41). Numbers and Stephens (1998: 74) noted that "a generally overlooked factor that contributed to the outburst of militant antievolutionism in the South was the growing popularity of Darwinism among the educated classes in the region."

People in the United States seem to have greater problems understanding the concepts of evolution than citizens of any other country in the West. Difficulties in apprehending these fundamental biological principles stem from inadequate education, particularly in the sciences but in other areas as well, and from the long-standing belief in the account of creation given in the Book of Genesis, a belief reinforced by the purveyors of ultraconservative religious doctrines. It is little understood by the public at large that an appreciation of evolution is basic to an overall understanding of the biological sciences and undergirds all research in those disciplines. Consequently, efforts to suppress the spread of evolutionary ideas are anti-intellectual, misguided, foolish, and in some instances probably perverse. Attempts to restrict or prevent the teaching of evolutionary theories are clear evidence that many do not grasp the idea of academic freedom. A poorly educated public, religious conservatism, and an inadequate understanding of academic freedom, factors that are not entirely independent, feed upon one another to varying degrees, producing an environment that is often unfriendly to activities of the intellect.

Contemporary Events

Relatively recent acts emanating from the legislatures of two states are reminders that the United States is intellectually not very far removed from the early 1920s. During the 1980s the Federal courts ruled as unconstitutional acts passed by the legislatures of Arkansas and Louisiana that would have required the teaching of "creation science"
along with evolution in the public schools of those two states (Berra, 1990: 134-138; Numbers, 1992: 249-251; Webb, 1994: 228-253). Perhaps often seen as more of a southern phenomenon than a nationwide one, the contemporary antievolution activity, or creationist movement, is far from being geographically restricted. In the United States, the most influential advocates of that movement seem to be associated with the Institute for Creation Research in El Cajon, California, and/or the Creation Research Society, "the leading creationist organization of the late twentieth century" (Numbers, 1992: 215). During the latter part of the twentieth century no one has done "more to popularize scientific creationism than Henry M. Morris [b. 1918] and his colleagues at the Institute for Creation Research in greater San Diego" (Numbers, 1992: 121, 283).5

For Ohio, a state usually thought of as one of the more progressive, one finds disturbing statistics on the lack of scientific sophistication among its residents. Berra (1990: 122) reported that

well over half the biology graduate students surveyed at The Ohio State University favored teaching creationism in public schools.

Another survey showed that only 12 percent of Ohio's high school biology teachers could select from five choices the phrase that best described the modern theory of evolution!... In an equally alarming survey of 730 Ohio school board presidents... which brought 336 responses, 53 percent felt that "creation science" should be favorably taught in public schools, and most of this group felt it should be presented in biology or science classes. Less than 2 percent of the school board presidents were able to correctly select the statement that best described the theory of evolution from a list of five choices. Nearly 50 percent indicated they would do nothing if they learned that "creation science" was favorably taught in science class in their district, and 57 percent indicated that the school boards themselves should determine whether "creation science" or evolution should be included in science classes.6

A survey conducted at Oberlin College in Ohio, "a highly selective, independent, coeducational institution," showed that 56 per cent of the students responding felt that creationism should be taught in the public schools (Zimmerman, 1986: 134-136). "The crisis in science education is certainly alive and well in Ohio" (Berra, 1990: 122). And I might hasten to add, that it is also doing well elsewhere in the United States, as is obvious from "numerous reports of teachers advocating creationism" and attempts "to introduce anti-evolutionary or explicitly pro-creation materials into science classes" (Futuyma, 1995: 251). Displaying an abysmal lack of scientific understanding, one school superintendent chose to glue together the pages in a textbook that described the Big Bang Theory (but offered no alternative explanations), rather than run the risk of offending the sensibilities of elementary school students and their parents (Storey, 1997: 68).7

Perhaps, more surprising is the revelation that the influence of the antievolutionists reaches even into the Federal funding agencies.

The anti-evolutionary climate is so threatening that at the National Science Foundation, the largest Federal agency that funds basic scientific research, the titles of research projects are allegedly often altered to replace the word "evolution" with words that are less likely to evoke hostile responses—and funding cuts—from conservative members of Congress (Futuyma, 1995: 252).

In June 1987, in Edwards v. Aguillard, the Supreme Court declared unconstitutional the law requiring the teaching of "creation science" along with evolution in the public schools of Louisiana. Shortly thereafter the sentiments of the antievolutionists attracted the attention of official Washington. Despite clear evidence of the extremely poor preparation in science that is typical of students in the United States, the science education programs of the National Science Foundation "remained vulnerable to political pressures." Recognizing that members of Congress and their aides were, in general, ignorant of scientific and technological issues and easily swayed by the jargon-filled arguments of the creationists, and as a consequence prone to political decisions for disputes arising from the evolutionist-creationist conflict, the officials at the National Science Foundation "tacitly agreed to sacrifice science education programs to maintain support for their many other endeavors" (Webb, 1994: 248, 253-254).

That most members of Congress know little of science is certainly not surprising, in view of the fact that the vast majority of those who elect them have almost no scientific awareness. A number of surveys conducted during the late 1980s showed in bold relief the very poor quality of science education in the United States. In the summer of 1988, only 12 percent of those responding to a poll "agreed with the statement that astrology was 'not at all scientific.'" More than a fifth of the more than 2,000 adults interviewed during a survey by Northern Illinois University "believed that the sun revolved around the earth" and "less than half of all respondents knew that the earth revolved around the sun once a year, with an incredible 36 percent answering that they did not have any idea how often the earth revolved around the sun." Workers from the University of Texas at Arlington surveyed 400 biology teachers throughout the country, and, among other distressing findings, learned that 27 percent thought it "possible for the living to communicate with the dead" (Webb, 1994: 254).

Clearly, then, better overall training in science, an
understanding of evolutionary biology, and knowledge of the history of the evolution-creationism controversy are sorely needed throughout the country. How do we turn things around? That question is not merely rhetorical; it is a question in dire need of being addressed and addressed promptly. First of all we need to be honest. As pointed out by Storey (1997: 69), it is long past the time when we can afford to take the easy road and blame public school teachers, politicians, or parents for the sorry state of science education in the United States. College science professors are equally, if not more, culpable.

Who teaches the last biology course to most of the future school board members, the school administrators, the politicians and the journalists—people who combine to shape public opinion and set policy? We do. Are we collectively doing a good job with scientific methods and evolution? The honest, inescapable answer is no (Storey, 1997: 69).

The culpability of science professors may rest more with their complicity or acquiescence in lowering the quality of curricula than with any classroom deficiencies. In 1997, "only a third of universities and colleges require[d] students to take at least one course in the natural sciences" (Wilson, 1998a: 13).

Surprisingly, perhaps, the reach of creationism extends well beyond the borders of the United States, stretching into Latin America, Canada, Great Britain, continental Europe, Africa, much of Asia, Australia, and New Zealand (Numbers, 1992: 323-335).

Unlike the antievolution crusade of the 1920s, which remained confined mainly to North America, the creationist revival of the last third of the century rapidly spread overseas as American creationists and their books circled the globe. By the 1990s scientific creationism, though made in America, had become a small-scale international phenomenon (Numbers, 1992: 325).

Until relatively recently, attacks on evolutionary biology came almost entirely from right-wing religious. Now it seems that the academic left has joined the conflict, being especially exercised by evolutionary explanations for attributes of human behavior or culture, with many social theorists allowing innate biology only in a constraining role—"a set of natural limits on human functioning" (Ehrenreich and McIntosh, 1997: 12). Ehrenreich and McIntosh (1997: 12) have called the extreme form of left-wing enmity to biology "secular creationism," which is "a creed that denies our biological heritage has anything to do with what people want or how they act" (Cartmill, 1998: 82).

Like their fundamentalist Christian counterparts, the most extreme antibiologists suggest that humans occupy a status utterly different from and clearly "above" that of all other living beings. And, like the religious fundamentalists, the new academic creationists defend their stance as if all of human dignity—and all hope for the future—were at stake (Ehrenreich and McIntosh, 1997: 12).

The academic left, composed mainly of humanists and social scientists, has not limited its attacks to evolutionary biology but has taken on the much larger task of excoriating the natural sciences in general. Assaults from a group that knows little of what it assails would hardly warrant notice other than bewildered amusement if the attacks did not have potentially serious consequences. "Outside the community of professional scientists and engineers, understanding of even the most elementary science is thin and vague" (Gross and Levitt, 1994: 3, 7, 244). Against such a background, the pronouncements of the scientifically illiterate academic left have the potential of doing great mischief.

The teaching of evolution is inextricably intertwined with the larger issue of academic freedom. Accordingly, I have devoted some space to that larger issue as it relates to South Carolina. Academic freedom could be defined as the freedom to search for the truth in whatever direction the search may lead and to proclaim the results of the search without interference or fear of interference. Academic freedom was certainly at issue when James Woodrow lost his position at Columbia Theological Seminary, while simultaneously maintaining his place at South Carolina College, and was probably unappreciated many years earlier when Thomas Cooper disclosed his unorthodox theological ideas. Those who have been the beneficiaries of academic freedom are enormously indebted to Thomas Cooper, James Woodrow, and others like them who strove courageously for the right to declare the truth as they saw it. Men such as A. C. Moore, who were not as outspoken as either Cooper or Woodrow, but who held the search for truth in high regard, have also helped to shine the light into the nooks and crannies of the intellectual landscape that would have otherwise been obscured by darkness.

With the preceding in mind and being aware that the story of the controversy is engaging, needs to be understood, and is often times amusing, I offer an annotated version of Moore’s essay that he entitled “Evolution Once More.” Displaying remarkably modern ideas that deserve wide circulation, Moore’s composition is an objective view of the intellectual atmosphere of his day, not only in his native state but also in the country as a whole. In order to place Moore’s effort in proper perspective, I present biographical sketches of him, of James Woodrow, a multifaceted man who greatly influenced Moore, and of Thomas Cooper, an iconoclastic genius, who courageously fought for the freedom of thought and inquiry and helped to prepare the way for men like Woodrow and Moore.
Thomas Cooper (1759–1839; Figure 1)

An early 19th-century resident of Columbia who fought valiantly for academic freedom, and who could have served as a role model for those who followed, was the brilliant scholar Thomas Cooper, who became the second president of South Carolina College (now the University of South Carolina) in December 1821 and served in that capacity until January 1834. Born in London (Westminster) on 22 October 1759 and educated at Oxford and in London, Cooper studied medicine, law, chemistry, and philosophy and came to the United States in 1794, practicing both medicine and law for a number of years. His contributions to science were greatest in chemistry. In addition to editing a number of European textbooks of chemistry for American students, he is noteworthy for the preparation of potassium (apparently the first to do so in America) and chlorine (for use in bleaching). Cooper had a special talent for becoming embroiled in disputes, having been involved in controversies in England, France, and other parts of the United States before arriving in South Carolina early in 1820. While President of the College, he taught a wide variety of courses—including chemistry, mineralogy, geology, belles lettres, criticism, logic, and political economy—a testament to the universality of his intellect and to the vastness of his learning. A man of heterodox religious views, he did not endear himself to the church-going people of South Carolina, particularly the Presbyterians who were very influential, when he proclaimed that the Mosaic version of the creation of the Earth was incorrect and that Moses did not write the Pentateuch, scoffed at the Noachian Flood, and authoritatively asserted that it was impossible for the Earth to have been created in six days. Such positions and others, some of which must have been even more disturbing to those who took their Bible literally, infuriated the Presbyterians, and their considerable influence led to investigations of Cooper by legislative committees in 1822 and 1823 and by the Board of Trustees of South Carolina College in 1831–1832. Cooper emerged victorious from all of those fights, exonerated of the charges brought against him, but he had grown tired of the fray and submitted his resignation as President in November 1833, remaining for an additional year as a lecturer in chemistry (Elder, 1947: 484; Hollis, 1951: 74–82, 98–101, 107–116; Malone, 1961: 4–10, 252–253, 337–367; Dictionary of Scientific Biography, 1971, Vol. 8: 399–400; Greene, 1984: 170). Cooper died on 11 May 1839 and is buried in the yard of Trinity Episcopal Cathedral near the College he served so well.

Controversial even in the grave, he rests under a monument which reads in part, "ERECTED BY A PORTION OF HIS FELLOW CITIZENS" (Hollis, 1951: 118).

Malone (1961: 399–400) noted that "perhaps no man of Cooper's generation did more than he to advance the cause of science and learning in America."

In chemistry, geology, and economics, he was distinctly a pioneer in America, and his formal and informal discussions of educational aims and problems reveal a statesmanship which would have made him conspicuous in any generation (p. 400).

Regardless of the intrinsic merit or demerit of his philosophical position, his advocacy of the free discussion of all subjects whatsoever entitles him to a conspicuous place in the history of intellectual liberty in America. His fears of the designs of the clergy were often hysterical, and at times he was himself intolerant, but his implacable hostility to all forms of bigotry and his insistence that the march of mind be unimpeded have left humanity his debtor. His emphasis upon the historical method as applied to the sacred writings was noteworthy for its day, and strikingly prophetic. Many others may have thought as he did, but very few showed equal courage in expressing their opinions (p. 399).

The University of South Carolina has memorialized this intellectual giant and courageous iconoclast by naming the main library on the Columbia campus the Thomas Cooper Library.
James Woodrow (1828–1907; Figure 2)

Born in Carlisle, England, on 30 May 1828, James Woodrow sailed from Liverpool in November 1835 with his parents, siblings, and a maternal aunt, bound for New York, eventually settling with his family in Chillicothe, Ohio. After graduating in 1849 with highest honors from Jefferson College (Canonsburg, Pennsylvania) and teaching for several years in academies in Alabama, he accepted, in 1853, a position as professor of natural sciences at Oglethorpe University, a small Presbyterian college near Milledgeville, Georgia (now located in Atlanta). During the summer of 1853, before beginning his duties at Oglethorpe, he studied under Louis Agassiz at the Lawrence Scientific School at Harvard and then received a leave of absence from Oglethorpe, which he used to study at Heidelberg. In 1856 Woodrow received, summa cum laude, the degree of Doctor of Philosophy (presumably in chemistry) from the University of Heidelberg. Although offered an opportunity to lecture at Heidelberg, he refused it in favor of returning to Oglethorpe, teaching there until 1861. During his tenure at Oglethorpe, Woodrow became engaged in mission work among the churches in the vicinity of Milledgeville. Convinced that he should preach on a regular basis, he undertook privately the study of Hebrew and the necessary theological subjects. Woodrow became an ordained Presbyterian minister, preaching at humble country churches near Oglethorpe, sometimes taking along his favorite student, Sidney Lanier (1842–1881), who would become one of the best known American poets (Elder, 1947: 485–486; Hollis, 1956: 166; Eaton, 1962: 3–4; Dictionary of American Biography, 1964, Vol. 10, Part 2, p. 495; Heckscher, 1991: 7–8; Numbers and Stephens, 1998: 61). Years after his student days at Oglethorpe, Lanier remarked “that he owed to Professor Woodrow the strongest and most valuable stimulus of his youth” (Anderson and Starke, 1945: 19).

In 1861 Woodrow accepted the newly founded “Perkins Professorship of Natural Sciences in Connexion with Revelation” at the Columbia Theological Seminary, a Presbyterian institution, in Columbia, South Carolina (now in Decatur, Georgia) (Eaton, 1962: 4). The purpose of the professorship “was to evince the harmony of science with the records of our faith, and to refute the objections of infidel scientists” (Dictionary of American Biography, 1964, Vol. 10, Part 2, p. 495). In his inaugural address as Perkins Professor, Woodrow mentioned that there was not “a single similar chair in any theological school either in America or Europe, to serve as a model” and noted the points of disagreement between revealed religion and science that he planned to treat in his lectures. Among those points were the age of the Earth, the subject of chronology, and the length of man’s presence on Earth. The subject of evolution was not mentioned; Darwin’s Origin of Species, having been published only two years earlier in 1859, was little known in the South before the American Civil War (Eaton, 1962: 5).

With the outbreak of the Civil War, the Seminary was forced to close because the entire student body volunteered to serve in the Confederate Army. Woodrow also volunteered his services to the Confederacy, becoming “chief of the Confederate chemical laboratory in Columbia” (Eaton, 1962: 5), zealously aiding “the Confederacy in the manufacture of explosives as well as medicines” (Elder, 1947: 488).

From 1861 until 1885 Woodrow edited and published The Southern Presbyterian Review, a quarterly journal, and from 1865 until 1893, Southern Presbyterian, a weekly periodical; he also operated a successful commercial printing business. In addition to teaching at the Seminary, he served as a science professor at South Carolina College for many years (1869–1872; 1880–1897) and was President of that institution from 1891 to 1897. Despite all of his teaching and publishing commitments, Woodrow somehow found time to engage extensively in business, functioning in executive positions with a bank, a building and loan association, a land and investment company,

Although Woodrow had superb credentials as a scientist, his chief published works dealt with religious topics. Consequently, he would not have been expected to become the central figure in a dispute that developed in the Presbyterian Church in 1884. While traveling in Europe in 1872-1873, Woodrow discussed Darwinism with many scientists and found that almost all of them were receptive to the new theory. Nevertheless, being strongly influenced by his old mentor, Louis Agassiz, the best-known scientist opposing Darwinian theory in North America, Woodrow did not accept it, hoping instead that scientists in the United States would lend support to his position (Eaton, 1962: 8). However, a number of very hostile attacks on science moved him to publish rebuttals (Woodrow, 1865, 1873, 1874) to articles, especially those of the theologian Robert Lewis Dabney (1820-1898), opposing the findings of the physical sciences (Elder, 1947: 488-494; Eaton, 1962: 6-8; Numbers, 1992: 14). In an article entitled “Geology and its assailants,” Woodrow examined the classes of combatants engaged in the war against geology, observing that while we have undoubting faith in the word of God, we have equal confidence in our ability to interpret it, and are influenced by that intolerance towards all who believe either less or more than ourselves, which is the disgrace of our kind (Woodrow, 1863: 550).

Woodrow’s perspective of science during this period was summed up well by Eaton (1962: 7).

Science is neither religious nor irreligious, Woodrow maintained; there is no Christian law of gravity; the events of nature must be accepted as produced by natural laws unless proved otherwise, that is by the Holy Scriptures.

Despite the fact that Woodrow to that point had not been an advocate of evolutionary theory, members of some of the Presbyterian synods suspected “that Professor Woodrow was unsound in the faith in regard to the theory of evolution” (Eaton, 1962: 9). As a consequence, the Board of Directors of the Columbia Theological Seminary passed a resolution on 10 May 1883 asking Woodrow to publish in The Southern Presbyterian Review his views on evolution “as it respects the world, the lower animals, and man” (Eaton, 1962: 9). Woodrow was stimulated by that request to review the evidence for evolution; his review led him to change his position on the subject. He no doubt understood the perils of proclaiming his support of Darwinian theory, but in spite of that, he addressed the Alumni Association of the Seminary on that subject on 7 May 1884 (Eaton, 1962: 9). At the requests of the Alumni Association and the Board of Directors of the Seminary, his address was published in the July 1884 issue of The Southern Presbyterian Review. In an attempt to persuade his audience of the validity of his position, Woodrow observed that in view of all the facts now presented—the way in which animals have succeeded each other, beginning as far back as we can go, and coming down to the present; the series of resemblances which connect them from the lowest to the highest, exhibiting such remarkable unity of plan; the existence of rudimentary organs; the geographical distribution of animals, and the close connexion of that distribution now and in the past—in view of all these facts the doctrine of descent with modification, which so perfectly accords with them all, cannot be lightly and contemptuously dismissed.

Then he noted that in the enumeration made, I have been careful to state none but well-ascertained facts, which any one who wishes to take the time can easily verify. Are not the coincidences such as must almost compel belief of the doctrine, unless it can be proved to be contradictory of other known truth? For my part I cannot but so regard them; and the more fully I become acquainted with the facts of which I have given a faint outline, the more I am inclined to believe that it pleased God, the Almighty Creator, to create present and intermediate past organic forms not immediately but mediately, in accordance with the general plan involved in the hypothesis I have been illustrating.

Further on he stated that believing, as I do, that the Scriptures are almost certainly silent on the subject, I find it hard to see how any one could hesitate to prefer the hypothesis of mediate creation to the hypothesis of immediate creation. The latter has nothing to offer in its favor; we have seen a little of what the former may claim. . . .

As he brought his comments to a close, Woodrow remarked that

I have now presented . . . my views as to the method which should be adopted in considering the relations between the Scriptures and natural science, showing . . . that the contents and aims of the Scriptures and of natural science are so different that it is unreasonable to look for agreement or harmony . . . that there are many good grounds for believing that Evolution is true in these respects; and lastly, that the reasons urged against it are of little or no weight. . . . The doctrine of Evolution in itself . . . is not and cannot be either Christian or anti-Christian, religious or irreligious, theistic or atheistic . . . (Woodrow, 1884: 366-368)

In September 1884, the board of directors met and debated what should be done about the presentation of such ideas in the Seminary. Woodrow won this first battle
in what would eventually become known as the "Woodrow War," temporarily retaining his freedom to teach evolutionary theory in the Seminary as a result of an eight to nine vote in his favor. His short-lived success was apparently largely due to his stated belief in the inerrancy of the Bible, although he simultaneously maintained that the concepts of evolution did not contradict Holy Writ. Despite Woodrow's acknowledgment of the infallibility of the Scriptures, the conservatives in the Presbyterian Church persisted in their attempts to have him removed, and he was dismissed from his professorship in December 1884. Reinstated in December 1885, the board of directors, by a unanimous vote, dismissed him again in December 1886. That battle was not the end of the war, however; Woodrow carried the fight further by appealing to the highest court of the Southern Presbyterian Church, the General Assembly. His appeal was heard in May 1888 at the Assembly's Baltimore meeting, but it was turned down by a vote of 139 to 31 (Hollis, 1956: 166; Eaton, 1962: 9–13; Numbers and Stephens, 1998: 63–64). If the Church had seen fit to heed the recommendation of John Calvin, as quoted by Woodrow (1884: 351), the entire controversy might have been avoided. Calvin stated that "he who would learn astronomy and other recondite arts, let him go elsewhere" [than the Bible].

In a letter written to D. H. Chamberlain (apparently in mid-1891), Woodrow described his position in the dispute with the leadership of the Presbyterian Church.

I would have resigned my seminary professorship at the beginning of the controversy, as soon as I found my views were unacceptable, if it had been possible for me to do so honorably. But my resignation was demanded on the ground that my teaching was inconsistent with the system of doctrine contained in our Confession of Faith. I thought (and think) that my resignation would have been an admission of the truth of the ground, hence my refusal.

Woodrow's position was not only unorthodox in the view of his colleagues in the Presbyterian church but also inconsistent with the mainstream of biological thought of his day.

In presenting his own beliefs as to evolution, Woodrow made a startling distinction between the creation of Adam's body and of Eve's body. The anatomy of the human male, he maintained, was evolved from the lower animals, but that of the female was directly created by a miracle of God. His reason for making this fantastic distinction was that the Bible had clearly stated the mode of creation of Eve's body but was silent as to the process of the creating of Adam's body. Thus Woodrow must be regarded as a transitional figure, who clung to the old pattern of thought while entering the threshold of the modern world of science (Eaton, 1962: 11).

It seems most likely that James Woodrow was (and still is) without peer in simultaneously holding positions in the camps of both the evolutionists and Biblical literalists.

Luckily, the "Woodrow War" had no effect on his faculty position at South Carolina College and was not at issue when he was chosen president of the institution in 1891, even though the trustees of the College were well aware of Woodrow's participation in that religious controversy (Hollis, 1956: 166–167; Stephens, 1994: 73).

The brouhaha that erupted over the Woodrow case drew national attention from periodicals such as Popular Science Monthly, The Nation, and American Naturalist during the long years it took the affair to wind its way through the halls of governance of the Presbyterian Church. Because of the considerable publicity accorded the "Woodrow War," many people in the United States were led to believe that "heresy trials and dismissals" belonged exclusively to the domain of conservative churches in the South, but such was not the case. For example, an Episcopal priest in Canton, Ohio, Thomas Howard MacQueary, published a book in 1890 entitled The Evolution of Man and Christianity that generated a firestorm in the Episcopal Church and led to his trial for heresy in 1891 and departure from the Episcopal clergy (Webb, 1994: 35).

Woodrow's brother-in-law, the Reverend Joseph Ruggles Wilson (1829–1903), became a member of the faculty of the Seminary in Columbia in 1870 (Heckscher, 1991: 6, 19, 140–141). Among the four Wilson children was a youth named Thomas Woodrow, destined to become well known as an educator, politician, and statesman. In the Woodrow papers at the South Caroliniana Library, there is a large formal invitation to James Woodrow to attend the inauguration in 1902 of his nephew, Woodrow Wilson (1856–1924), as President of Princeton University. Unfortunately, Woodrow did not survive to see Wilson inaugurated as the 28th President of the United States in 1913. After James Woodrow's death on 17 January 1907, Woodrow Wilson in a letter to a friend described his uncle as one of the noblest men he had known:

A man of many small failings, I am glad, for my own comfort, to remember, but a man made to love (in the quiet, self-contained Scottish fashion, but very, very deeply, none the less) and to be loved, and gifted in an extraordinary degree with the powers that make a great thinker and a great man of science. He followed duty to obscure places and kept himself in mere faithfulness from the eye of fame; but his friends and intimates knew him for a man who might have placed his name among the great names of our men of learning. It pleases me to think of the gracious and helpful influences he has brought into the lives of many generations of students, and not the least into the life of a nephew who never told him how much he owed to him (Link, 1974: 17).

The historian Clement Eaton made James Woodrow and academic freedom in the South the subject of his Presidential address to The Southern Historical Associa-
tion in November 1961 (Eaton, 1962). In summing up Woodrow’s contributions, Eaton (1962: 17), mentioned that, as noted by Lord Acton (1834–1902), the Roman Catholic historian, “Tolerance ... is the delicate fruit of a mature society” and academic freedom, likewise, is the product of maturity, a stage of culture that has been reached through growing pains and the struggles of generations of teachers who have preceded us. In the attainment of the large measure of freedom of teaching which we enjoy, the subject of my paper, James Woodrow, played a significant and triumphant role. I salute his memory, and hope that should any of us ever face a similar crisis of academic freedom, we ... may display his great moral courage.

A testament to the high regard in which Woodrow was held at the University of South Carolina can be seen in the naming in his honor of a new dormitory that opened in 1914 (Hollis, 1956: 265).

Andrew Charles Moore (1866–1928; Figure 3)

Andrew C. Moore was born in Spartanburg District (now County), South Carolina, 27 December 1866, and entered South Carolina College in 1883, graduating with an A.B. in 1887. For eleven years he was an administrator in public schools in South Carolina and Alabama and in 1898 began graduate studies at the University of Chicago, where he was a fellow in biology and an assistant in botany. Moore was appointed Assistant Professor of Biology, Geology, and Mineralogy at South Carolina College in 1900 and was promoted to full professor in 1903. South Carolina College became the University of South Carolina in 1906, and A. C. Moore was in charge of a separate department of biology at that institution from its inception until his death in 1928. In addition to teaching, Professor Moore served for some years as Dean of the University and on two occasions as acting President. In acknowledgment of his accomplishments, Wofford College in Spartanburg, South Carolina, awarded him an LL.D. in 1909 (Hollis, 1956: 216, 243, 264; Herr, 1984: 106–107).16

Moore completed most of the work for his doctorate at Chicago under the direction of John M. Coulter17 but did not finish his dissertation (Hollis, 1956: 264; Herr, 1984: 106), part of which was published in the Botanical Gazette (Moore, 1903, 1905). While at the University of Chicago, Moore studied the development of the embryo sac of the plant *Lilium philadelphicum,* but never published his results. A prepared slide bearing a label in Moore’s handwriting which states “Lilium philadel. 1st meiosis 2nd meiosis ACM Feb ’99” indicates a use of the term “meiosis” well before “its historically recognized origin and publication by J. B. Farmer and J. E. S. Moore (no relation to A. C. Moore)” (Herr, 1984: 107; Battaglia, 1985: 121–122). In introducing that term into the scientific literature, Farmer and J. E. S. Moore (1905) used the incorrect form “maiosis”—an error that would have been unlikely for A. C. Moore, who knew Greek well. A. C. Moore never used “meiosis” in a publication, and, as a consequence, his important contribution to the vocabulary of biology was overlooked and attributed to others until Herr pointed out its true authorship in 1984 (Battaglia, 1985: 102, 121, 127–128).

In the 1920s Moore became interested in the implications of the dispute between evolutionists and religious Fundamentalists, a dispute exacerbated by the Scopes Trial in 1925. Reading about the Trial, Moore no doubt remembered the extremely unpleasant experience endured by James Woodrow some 40 years earlier. In fact Moore was in the audience when Woodrow gave his address before the alumni of Columbia Theological Seminary in May 1884, being at the time a freshman at South Carolina College. Moore’s impression of Woodrow was that of an earnest and able scholar who had devoted years of study to a subject and on that occasion gave expression to
the deliberate conviction that a certain scientific theory was probably true, notwithstanding the fact that it seemed to be in conflict with the Sacred Scriptures... . His explanation... that the Bible did not teach scientific truth and was never intended to do so... appealed to me as reasonable and the acceptance of his theory gave me no concern— did not upset my religious convictions. 18

In a number of letters, written while continuing studies in botany and genetics at the University of Chicago during the summer of 1925, Moore expressed the attitude of the scientist towards the controversy between the advocates of evolution and the proponents of creationism. In a letter to his wife, postmarked 25 July 1925, Moore wrote:

I can't help feeling a heavy sense of responsibility to the youth who may come under my influence, especially at this critical time of religious unrest. I fear the fundamentalist agitation has gone too far and harm will be done. Mr. Bryan in his zeal has set going forces that he knew not of and that I fear will do incalculable harm. Unless the leaders in the church awake to the gravity of the situation and stop this effort to legislate men into the straight & narrow path, I fear the pendulum is going to swing in the opposite direction... What the churches should be doing is to encourage in every way the study of science to find out what is true and what is false and when truth is discovered to make it fit in with religious conceptions. It is no less than criminal for a man to denounce the findings of science when he knows nothing about it & glories in his ignorance. 19

But Moore had not always felt as comfortable with expressions of opinions that might rankle the Fundamentalists (at least not with those voiced in public), for in 1909 he had asked a visiting lecturer to take care in commenting on evolution. "Though we have made progress toward... evolution since Dr. Woodrow's time... we have hardly reached the point where we could make the subject too prominent" (Hollis, 1956: 246).

No thinking man would criticize the University for teaching evolution, the dean added; but there were still many "mossbacks" in South Carolina, and the denominational colleges would gladly take up anything which could be used to injure the University (Hollis, 1956: 246).

On 17 September 1928, A. C. Moore died 20 while still active in academic affairs, having served his University and State with distinction. He indeed was a stalwart in maintaining the often frail intellectual bridge that spanned the difficult times between 1865 and the end of the Second World War. Moore's many contributions have been recognized appropriately. The herbarium in the Department of Biological Sciences at the University of South Carolina, initially developed by Moore, has been named the Andrew Charles Moore Herbarium. 21 That repository held 76,500 specimens in mid-March 1999, a few hundred of which were collected by Moore. 22

The Moore Manuscript of 1923

The draft of Moore's manuscript in the South Caroliniana Library is obviously not a finished product because it contains a number of handwritten emendations and some lapses that the author did not correct. Consequently, in a number of places, I have corrected minor typographical errors, modified the punctuation slightly, and made other small changes that improve the consistency and/or readability of the text, but I have in no way altered the meaning of the original. Additionally, I have supplied end notes identifying individuals, clarifying and/or elaborating on certain items, and correcting a few errors.

Moore read his manuscript, "Evolution Once More," at a meeting of the Kosmos Club, a town-and-gown organization in Columbia, of which Moore was a charter member and president in 1905-1906. His paper was so well received that a second entire evening's meeting was devoted to discussing it. 23 I do not know if Moore ever considered publishing his manuscript, but some of the comments made therein and the general tone of his essay lead one to speculate that he may have entertained ideas of distributing his document in some manner. On the other hand, in view of the antievolution sentiment that seemed to be sweeping much of the country at the time, he may have been satisfied to have his comments go no further than the ears of the members of the Kosmos Club, certainly a group more sophisticated and open to unconventional views than the general public. Perhaps he did not want to follow too closely in the footsteps of James Woodrow or Thomas Cooper and run the risk of becoming entangled in a never-ending disputation with those who had little knowledge, but much fear, of science and what it teaches. Be that as it may, Moore's treatise exhibits a modern point of view and a mind completely open to the discoveries of science, surprising, perhaps, taking into account his long years of dedicated service as an elder in the Presbyterian Church in both Birmingham and Columbia. 24

Evolution Once More 25

by

Andrew Charles Moore

I well remember how, as a small boy, just introduced into the study of geography, I at first refused to accept the statement that the earth is round like an orange or a ball. I remember discussing it with my companions on the school grounds— outside the sacred precincts of the schoolroom—and reaching the firm conviction that the statement was erroneous. I thought some man who was making a book was trying to "put something over" on me.
It couldn’t be true because it belied all my observations and experience. How could houses and trees stand upon anything except a flat surface? How could men and animals walk upside down on the other side of the world? Why wouldn’t ships slip over the curved surface of the ball and be lost? Besides, I could see with my own eyes that it was flat. I hadn’t traveled widely, but I had been to my grandmother’s, fourteen miles away, and it was flat there. My father had been to Charleston and it was flat there. Moreover, he had been to Virginia during the War and had fought all over that state and from the stories he told, I judged that it must be flat there also.

As I now look back upon my youthful skepticism, I am convinced I was quite right in my position, for I was basing my conclusion on evidence, but I would not have been justified in closing my mind at the time and basing all my subsequent thinking and all my subsequent actions upon that conclusion.

Soon I discovered that there were some things about the earth I did not know, things that needed to be explained. I did not know that the shadow of the earth cast on the moon during an eclipse was circular in outline. Nor did I know that ships upon going to sea seemed to gradually sink beneath the horizon—their hulls first and finally their masts. I did not know that ships by sailing eastward or westward and keeping the same course had actually come back to their starting points. With this additional information before me I saw that my theory that the earth was flat could no longer be maintained.

The geography book after all must be correct and so I modified my views and accepted the doctrine of the sphericity of the earth.

Some years later I came to the South Carolina College with an all-too-meager stock of nature knowledge—not much more than I had picked up as a farm boy from the fields and woods and streams—and a much greater reverence for authority, because most of the knowledge I had was gained from books and I had been taught that makers of books were wise men. I had had little training which encouraged me to think, but much to increase my reverence for authority.

As a freshman in the spring of 1884 I heard some of the upperclassmen, to whom I looked up with great respect, discussing an address which Dr. Woodrow was going to deliver in the Presbyterian Church. It was to be on evolution and from what they said I judged there would be something of sensation about it. I had never heard of evolution before. I might have heard the word, but I did not know what it meant. From the wise seniors I gathered that it had something to do with man coming from a monkey, and so I decided to hear the address.

There was nothing sensational about the setting, nor in the looks or manner of the venerable and dignified lecturer. I do not now remember anything he said, but I have left certain distinct impressions. One was that here was an earnest and able scholar who had devoted years of study to a subject and on that occasion gave expression to the deliberate conviction that a certain scientific theory was probably true, notwithstanding the fact that it seemed to be in conflict with the Sacred Scriptures.

The lecture was evidently not desirous of in any way impairing the authority of the Holy Scriptures, for he most emphatically affirmed his faith in their integrity. His explanation of the apparent conflict between the theory he was advocating and the teachings of the Sacred Writings was that the Bible did not teach scientific truth and was never intended to do so. His contention appealed to me as reasonable and the acceptance of his theory gave me no concern—did not upset my religious convictions.

Why could not God make man out of protoplasm, or anything else, for that matter, in a million years, as easily as out of dust in one day and that the 6th day of creation at nine o’clock in the morning of October 23, 4004 B.C., according to the eminent authority, Dr. John Lightfoot, Vice Chancellor of Cambridge University? But the Scriptures say explicitly that all things were created in six days, presumably of 24 hours duration each. Do not the Scriptures also teach, or if they do not explicitly teach, do they not imply that the earth is flat and that it is in the center of the universe? I had already accepted the doctrine of the sphericity of the earth and the heliocentric theory of the solar system, both of which seemed to contradict the accepted view of Scriptural teaching. My conviction was confirmed that Dr. Woodrow was right in holding that the Bible did not teach science.

Some years later, when I reached the senior class, I listened to Dr. Woodrow’s lectures on geology and there again my knowledge of the earth was increased and the flood of new facts called for new explanations. The age of the earth was one of the problems that presented itself for solution. Was it created in six days by the fiat of the Almighty as I had been taught to believe in a pious home, or in some other way? I was now prepared to examine the evidence and base my conclusions upon it. I learned that there were certain chemical and physical forces operating upon the surface of the earth tending to modify it. Weather was causing rocks to decay and crumble, rain and running water were removing this loose material and depositing it at lower levels. Rivers were carving out their valleys and lakes and seas were being filled up. The evidence seemed to point to the fact that these things had been going on for a long time, and why not? Wouldn’t water always run down hill and hadn’t it always done so? Wouldn’t frost always crack rocks and wouldn’t acids always attack and destroy them? The idea gradually dawned upon me that the present configuration of the earth was the outcome of natural forces operating in a natural way for untold ages.

The intellectual gain I had now made was the apprehension of the doctrine of uniformitarianism, a doctrine first clearly promulgated by the great English geologist Lyell, who taught that the same forces that are operating now
have always been operating and that the true explanation of the past history of the earth is to be found only by interpreting past events in the light of the present.

If this doctrine be true, why could not the age of the earth be estimated? Take, for instance, the gorge of Niagara River. By actual observation the falls are receding at a rate of little more than three feet per year. At that rate how long would it require the river to carve out a gorge approximately ten miles long? A simple application of arithmetic to the problem gives the answer of 17,600 years; a period three times the supposed age of the earth. Moreover, an examination of the walls of the gorge shows that they were built up of sediment which must have required for its deposition under standing water a period far in excess of that required for carving out the gorge. Besides, there must have been a period of elevation between the deposition of the rocks and the beginning of their erosion.

The calculation of the age of Niagara River is by no means as simple a problem as this, but we at least have a method of attack, which, when all the facts are known, will give approximate results. If it required Niagara River 17,000 years to carve out its gorge 200 or 300 feet deep—200 or 300 yards wide and ten miles long, how long did it take Colorado River to carve out the Grand Canyon, 4,000 to 6,500 feet deep, several miles wide and 200 miles long? Certainly not less than several million years. And the great Mississippi River, with its more than 1,500 miles of length and its great wide valley stretching hundreds of miles in width, must be immensely older. These and other indisputable evidences of the great age of the earth are certainly in conflict with the supposed teachings of the Bible. All of the great generalizations of science, which have necessitated readjustment of modes of thinking, have been accepted only after long and bitter struggle. Witness the Copernican theory, the Newtonian theory, etc. In some cases the complete acceptance of a new conception comes only after the old generation with its congealed ideas has passed away and a new generation with a plastic mind takes its place. The evolution idea has been no exception to this general rule, and has won its way thus far through a bitter struggle.

Upon the publication of Darwin’s *Origin of Species* in 1859, his theory of evolution became the target for attack by conservatives of all classes, theologians and scientists as well. Soon, however, the scientists, who had been trained to sift, weigh and evaluate evidence, were convinced and the more philosophical and farseeing among the theologians also, but many, who could not, or would not, understand the evidence, held out. Many of them made themselves ridiculous. For instance, Mr. Gladstone, the eminent British statesman and philosopher that he was, charged that the theory of evolution relieved God of the labor of creating and unchangeable law discharged Him from governing the world. Huxley replied that Newton’s doctrine of gravitation and the science of physical astronomy did the same thing, after which the great statesman discreetly held his peace.

Dr. George D. Armstrong, a distinguished Presbyterian divine, who was attacking Dr. Woodrow’s position on the evolution question, displayed unparalleled ignorance of the subject he essayed to discuss, when he defined evolution thus:

*Evolution, a hypothesis which postulates the transformation of an oak, not immediately, but by successive variations, into a silkworm, a silkworm into a frog and a frog into a man.*

He confirms this understanding or lack of understanding of evolution in a book which he subsequently published, for he says:

*There must have been some plant which had reached the same stage of differentiation with the cabbage, that did occupy a place in the ancestry of the cow.*
The tragedy of it is that he used such statements as the basis of an argument before the Presbyterian General Assembly at Augusta [Georgia] and "got by" with it, so far as the great majority of the members was concerned.

But the pièce de résistance of this type of criticism is that presented by Bishop Keener35 of the Methodist Church in an address before the Ecumenical Council of Methodism at Washington in 1891. In what the newspapers described as an "admirable speech"; he refuted evolution doctrines by saying that evolutionists had only to make a journey of twelve hours from the place where he was then standing to find together the bones of the muskrat, the opossum, the coprolite and the ichthyosaurus.

For the last decade or two the position of evolution has become so strong that it has not been seriously attacked until very recently, and this time not by scholars, but by zealous religious propagandists. Training schools for religious teachers, such as the Moody Bible Institute of Chicago,35 have become the centers for disseminating anti-evolution propaganda. The dominant tone of these schools is not scholarly, but evangelistic, not critical, but devotional. They assume the inerrancy of the English version of the Bible and undertake to instruct their students in its use as the "sword of the spirit." No one questions their motives. They are deeply religious and are actuated by zeal for extending the beneficent influence of religion to all men. There could be no higher motive, but purity of motive and sincerity of belief do not always justify an act. I may have the best interest of my friend at heart and sincerely believe that the medicine I administer him will give him relief, but if I should be mistaken and give him poison, my good intentions only prove his undoing. Truth, in the final analysis, should be at the basis of all action.

A book by the Reverend Alexander Patterson36 [1903], entitled The Other Side of Evolution issued by the Bible Colportage Association of Chicago may be cited as an example of the modern type of attack upon the evolution idea. The book would not be worthy of serious consideration, but for the fact that it reaches and influences a wide circle of readers who are misled by its erroneous teachings. The author seeks to discredit the theory of evolution by quoting multitudes of isolated, unconnected statements selected from the writings of a large number of scientists whereby he shows inconsistencies and points out that where there is no agreement among the doctors, there can be no true diagnosis. He proves most conclusively out of their own mouths that the most pronounced evolutionists do not believe in their own theories. He mistakes recent criticisms of Darwin's views on the origin of the species as criticism of evolution, while, as a matter of fact, the critics of Darwin are as thoroughgoing evolutionists as ever Darwin was. The debate among modern evolutionists is not over the fact of evolution, but over its causes, its methods and its course.

Another book entitled Q.E.D.37 [Price, 1917] in which its author, Professor Price, claims to have demonstrated the falsity of evolution is perhaps more misleading than Dr. Patterson's book. Dr. Patterson is not a scientist as any reader of moderate penetration would see at a glance, but Professor Edward [actually George] McCready Price,38 M. A., Professor of Chemistry and Physics, Lodi Academy, California, author of Outlines of Modern Christianity and Modern Science, The Fundamentals of Geology, God's Two Books, Back to the Bible, A Text Book of General Science, etc., should speak with greater authority. His facile handling of a wide range of scientific knowledge dazzles the uninformed. He is equally at home in the domains of Chemistry, Physics, Geology and Biology. His book is well written and displays skill in the marshalling of his materials, but, unfortunately for him, he does not confine himself to the facts. A review of his book would be interesting but I cannot now undertake that and shall leave him for the time being to the tender mercies of Professor Taber.39 I mention him in this place because he has been widely quoted by a class of religious propagandists, including Mr. William Jennings Bryan, who are at the present moment waging a campaign against the teaching of evolution in state supported schools. His most effective argument is based upon the alleged fact that the geological record is misunderstood by all geologists except him; that the doctrine that fossils occur in a definite order of succession is no longer tenable.

The most recent movement against the teaching of evolution was vigorously inaugurated the early part of last year before the legislature of the state of Kentucky. Professor Arthur M. Miller40 in Science, February 17, 1922, says of the proposed legislation that it is the culmination of an active propaganda against evolution which has been carried on in the state for over a year by a number of the ministers of several of the Protestant denominations. The leader of these is Dr. J. W. Porter,41 pastor of one of the Baptist churches in Lexington, and judging from the expressions in the Baptist press, he has the backing of a large element in his denomination. He it was who received a letter of encouragement from William Jennings Bryan which he promulgated from the pulpit. From this letter we quote the following:

The movement will sweep the country and we will drive Darwinism from our schools. The enemy is already fighting. The agnostics who are undermining the faith of our students will be glad enough to teach anything the people want taught when the people speak with emphasis.

On Friday, January 20, Bryan was brought to Kentucky, where he made a number of addresses against evolution. The one at Frankfort was before a joint session of both
houses of the legislature. In this he advocated legislation against the teaching of Darwinism and kindred "isms." At the close of his address in Lexington a resolution was presented by Rev. W. L. Brock, another Baptist minister of Lexington, and ruled from the platform to have been passed, in which the general assembly was petitioned to prohibit "the teaching in the state schools of evolution, destructive criticism and every form of atheism and infidelity whatsoever."

Bills were accordingly introduced both in the Senate and in the House of Representatives. The House bill reads as follows:

By Representative George W. Ellis, Barren County.

An act to prohibit the teaching in public schools and other public institutions of learning, Darwinism, atheism, agnosticism or evolution as it pertains to the origin of man.

Be it enacted by the General Assembly of the Commonwealth of Kentucky:

Section 1. That it shall be unlawful for a teacher, principal, superintendent, president or anyone else who is connected in any way with the public schools, high schools, training schools, normal schools, colleges, universities or any other institutions of learning in this commonwealth, where public money of this commonwealth is used in whole or in part for the purpose of maintaining, educating or training the children or young men or young women of this commonwealth; for such teacher, principal, superintendent, president or other person connected directly or indirectly with such schools or institutions of learning to teach or knowingly permit the same to be taught; Darwinism, Atheism, Agnosticism, or the Theory of Evolution in so far as it pertains to the origin of man; and anyone so offending shall on conviction be fined not less than fifty nor more than five thousand dollars or confined in the county jail not less than ten days nor more than twelve months or both fined and imprisoned in the discretion of a jury.

Section 2. If any school, college, university, normal school, training school or any other institution of learning which has been chartered by the Commonwealth of Kentucky and which is sustained in whole or in part by the public funds of said commonwealth shall knowingly or wilfully teach or permit to be taught, Darwinism, Atheism, Agnosticism, or the Theory of Evolution in so far as it pertains to the origin of man, shall forfeit its charter and on conviction shall be fined in any sum not to exceed five thousand dollars. In all proceedings of forfeiture or revocation of charter, the holder thereof shall be given thirty days notice in which to prepare for a hearing to be attended by its representative or counsel.

The commonwealth or the accused may take such oral or written proof for or against the accused as it may deem it the best to present these facts.

This act to be in full force and effect from and after its passage and approval as provided by law.

After a sensational campaign, the bill was finally defeated by the narrow margin of one vote in a total of 83. A little later—March 10th (16th?)—a somewhat milder bill was introduced in the South Carolina Senate. It was proposed as an amendment to the general appropriation bill and reads as follows:

And provided further that no moneys appropriated for public education or for the maintenance and support of state supported institutions shall be used by or paid to any such school or institution teaching, or permitting to be taught, as a creed to be followed, the cult known as "Darwinism."

The amendment passed the Senate practically without debate, Senator Miller making the only address. Mr. Miller explained that the bill was not intended to apply to the Lamarckian or any other theory of evolution, but only to that of Darwin and to Darwinism only insofar as it is a "creed to be followed." He explained that in introducing the measure it was not intended to prevent the explanation of evolution as a scientific theory as a matter of general knowledge, but only to prevent the teaching of Darwinism as a "creed to be followed."

The amendment did not reach the House, but was disposed of in the conference committee. It did not attract much attention, but it is not certain that its defeat would have been so easy had a determined fight been made for it and had Mr. Bryan been called in to assist. It is not impossible that we may yet witness the spectacle of the legislature of South Carolina attempting to repeal a law of nature.

A campaign is now being launched in Minnesota, as the direct result of an address by Mr. Bryan. Reverend W. B. Riley, pastor of the First Baptist Church of Minneapolis, chairman of a committee, called a state-wide conference in St. Paul for October 26 at which meeting the following resolutions were passed:

Preamble—As American citizens we believe in the complete separation of church and state, and are opposed to religious teaching in public schools—higher or lower.

As those who wish to teach Christianity must support their private schools, we believe it but just that those who wish to teach anti-Christian theories should be forbidden the use of tax supported schools for propagating their opinions.

Whereas, The evolutionary hypothesis has come to be accepted by many American teachers, and is increasingly taught in the public schools of Minnesota, including high schools, our state normals and state university, and

Whereas, This hypothesis, after sixty-three years of study, remains wholly unproven, and has increasingly shown itself to be a foe to the Christian faith, denying as it does the veracity of the Scriptures,
Therefore be it resolved, That we, citizens of Minnesota, representing thousands of our fellow citizens, hereby utter our protest against this propaganda of infidelity, put off in the name of science, and we call upon the trustees of state institutions to demand of teachers a cessation of such teaching and the removal from our schools of such textbooks as favorably present the same.

We do this in the interest of true science vs. science falsely so-called; and in the interest of fair dealing.

We hold that the first amendment to the constitution of the United States, "Congress shall make no law respecting an establishment of religion," was never intended to be interpreted that the state should become sponsor for irreligion; and that it is manifestly unfair to impose taxes upon Christian taxpayers to inculcate teaching inimical to the Bible and destructive of civilization itself.

We have waited patiently for this hypothesis to either prove a truth or to pass from public instruction. Having now no prospect of either, we demand that the state shall prove its impartiality toward its citizens by dispensing with a subject that is utterly divisive; and is, in the judgment of thousands of its taxpayers, utterly false.

And we declare that if the school authorities prove derelict in the enforcement of the law relating to the teaching of religion or of theories subversive of the Christian faith, we will appeal to the legislature for the enactment of such laws as shall eliminate from our tax-supported school system this antiscientific and antiscr iptural theory of the origin of man and the universe.

Meanwhile certain churches, notably in Texas and Oklahoma, have been waging an active campaign against evolution and all theories of Biblical interpretation at variance with the time honored and popularly accepted literal interpretation. I quote from Science, May 12, 1922, page 515:

THE TEACHING OF EVOLUTION IN THE BAPTIST INSTITUTIONS OF TEXAS

The teaching of evolution in the Baptist denominational schools in Texas is being investigated as heretical. The denomination is strong in membership and maintains about 15 colleges and seminaries in the state, the chief of which is Baylor University at Waco. It appears that the trouble arose as the result of the publication in 1920, by the Baylor University Press itself, of an "Introduction to the Principles of Sociology," by Grove Samuel Dow, Professor of Sociology in Baylor University. The book is based upon the theory of evolution wherever it touches upon the biological aspects of sociology, although the term biological evolution is scarcely or not at all used in the text. At a recent conference of representatives of the Baptists of all parts of the state, such teachings were pronounced heresy, and a sweeping investigation is being made of all of the Baptist schools of the state to determine how much "heresy" is being taught. Professor Dow has resigned his position.

A somewhat related situation has existed at Southern Methodist University, Dallas, where the teaching of Dr. John A. Rice, Professor of Old Testament Interpretation, has created the severe opposition of a large part of his church. Dr. Rice's book, "The Old Testament in the Life of Today," looks upon the Old Testament as a series of independent historical papers, each subject to its own interpretation. Many are considered as having been revised by several authors before they have reached their present form. Each is regarded as a literary production, subject to all of the rules of literary interpretation; this introduces a personal factor into any understanding of the Old Testament, and completely does away with literal interpretations. Dr. Rice has also left his position, to become pastor of a Methodist church in another state.

S. A. R.

In protest against the attitude certain church courts are taking [the following is of interest]:

THE AGITATION AGAINST THE TEACHING OF EVOLUTION

PROFESSOR J. V. DENNEY, president of the American Association of University Professors, addressed on June 14 the following letter to the moderator of the conference of the Northern Baptist churches meeting in Indianapolis:

As president of the American Association of University Professors, I desire to call attention to the peril confronting our higher institutions of learning at the present time because of the "Fundamentalist" or "anti-evolution" movement which has appeared in two state legislatures and in the constituencies of several colleges controlled by or affiliated with the religious denominations.

Letters from presidents and professors indicate widespread anxiety lest the cause of higher education suffer serious injury through attempts at coercive measures, interfering with the professor's duty to teach the truth of his subject as determined by the body of past and present laborers in his own field and as confirmed by his own conscientious studies and researches. The chief injury is not merely to the professor who loses his position or to the particular institution that sacrifices a permanent aim to a passing fear. It is in the degradation of the office of teacher; in the establishment of distrust and suspicion in the public mind towards all colleges and universities; and in the immediate loss to both church and state of strong forces for good through the slackening of devotion and enthusiasm and the encouragement of casuistry, subtlety and insincerity among those who are called to teach with an eye single to truth.

The colleges controlled by or affiliated with religious bodies are public institutions in the sense that they solicit and receive students on terms common to all good colleges. They impose on applicants no political or religious tests. They forewarn the public of no doctrine in history, eco-
nomics, literature and the sciences that is essentially at variance with the body of free and accepted teaching in these departments of learning throughout the country. Their professors cooperate in the work of all of the learned societies, and are bound by the code of honor in scientific research and by the obligation of scrupulous honesty of statement in teaching. Any invasion of this high obligation is an attack on manhood in teaching and destructive to real education.

Any college or university, whatever its foundation, that openly or secretly imposes unusual restrictions upon the dissemination of verified knowledge in any subject that it professes to teach at all, or that discourages free discussion and the research for the truth among its professors and students will find itself shunned by professors who are competent and by students who are serious. It will lose the best of its own rightful constituency and will cease to fulfill its high ministry. The same results, disastrous to true education, will follow whether the restrictions are adopted voluntarily by the college itself, or are forced upon its administrative officers by the state legislature, an ecclesiastical body or by powerful influence operating through trustees. The question of legality and of good motive is also irrelevant so far as moral and educational results are concerned.

The five thousand members of the American Association of University Professors in active service in some two hundred colleges and universities of the United States are of one mind on the fundamental necessity of preserving the integrity of the teaching profession. They realize that their work is a sacred trust that can be fulfilled only in freedom of conscience, loyalty to the truth, and a profound sense of duty and of personal responsibility. They claim the support of all good Americans whatever their creed in resisting measures that will prove ruinous to our institutions of higher learning.\(^{(10)}\)

Mr. William Jennings Bryan\(^{(9)}\) seems to be the central figure in this recent crusade against evolution. However worthy his motives, or whatever his gifts, we cannot admit that Mr. Bryan is competent to discuss this question. It is a technical question involving the possession of special knowledge which Mr. Bryan clearly does not possess. He belongs to a generation which was educated under an old order in which the sciences had little place. He, therefore, has no first hand knowledge of the subject and draws his information, or misinformation, largely from Professor Price, who has no standing in the scientific world, and who stands practically alone among men claiming to be scientists in holding out against the theory of evolution, or from Dr. Alexander Patterson who is less well informed than Professor Price.

At the invitation of the New York Times, Mr. Bryan prepared an article for that paper in which he presented his argument against evolution. His article appeared in the issue of February 26, 1922, and was answered one week later by Professor Osborne of the National Museum\(^{(49)}\) and Professor Conklin of Princeton.\(^{(52)}\) From various press notices quoting some of Mr. Bryan's most striking sentences I looked forward with keen interest to the reading of the article in its entirety. I must confess to a feeling of great disappointment upon reading it and must think the Great Commoner is not at his best in cold type. With the inspiration of a great and responsive audience before him, no doubt his burning words of eloquence, interspersed with sparkling wit and withering sarcasm, would carry conviction to the great majority of his auditors, but for a critical examination of his views his written article, no doubt prepared with great care, best serves our present purpose. Let us analyze it in some detail.

He introduces his article with the statement:

The only part of evolution in which any considerable interest is felt is evolution applied to man. A hypothesis in regard to the rocks and plant life does not affect the philosophy upon which one's life is built.

He goes on further to state:

Evolution applied to fish, birds and beasts would not materially affect man's views of his own responsibilities, except as the acceptance of an unsupported hypothesis as to these would be used to support a similar hypothesis as to man. The evolution that is harmful—distinctly so—is the evolution that destroys man's family tree as taught by the Bible and makes him a descendant of the lower forms of life. This, as I shall try to show, is a very vital matter.

From these statements we may conclude that Mr. Bryan would be willing to accept a theory of evolution for all nature except man. Does the Biblical account of the creation justify such a position? Certainly not. If the Biblical account state that man was created in one day (the 6th), just as specifically does it state that the lower animals were created in one day (the 5th). If, as Mr. Bryan seems to admit, the Bible allows for the evolution of the lower animals, why does it not also allow for the evolution of man? But Mr. Bryan objects—man's origin must have been different because our philosophy of life demands it. But if evolution be the law of development, what becomes of a philosophy based on an exception to this law? Man certainly conforms to the law of development so far as individual development is concerned. He originates as a single cell, the ovum or egg, just as a starfish or a bird, or a rabbit; this cell is fertilized by another cell, the sperm, just as with lower animals; the fertilized ovum forms new cells by division, at first a spherical mass; then the cells in different regions begin to differentiate and soon tissues and organs begin to appear; and after a time the embryo takes on a recognizable form and finally comes forth and we say a child is born into the world. All the stages in the development conform in the minutest detail to the development of the beasts, or brutes as Mr. Bryan likes to call them.\(^{(53)}\) This is not a theory, but a fact.
To follow out the parallelism between man and the lower creatures in detail would weary you. Suffice it to say that man requires the same food stuffs as the lower animals, digests his food, absorbs and transports it, converts it into the living matter of his body and grows just as a rabbit or a sparrow. He breathes the same air, creates energy by the same chemical process of oxidation, moves by similar muscles and bones, is protected by a similar skin, reacts to cold and heat and light and hunger and the sexual impulses just as the beasts. With all this mass of evidence, and this is by no means all, how can we escape from the necessity of classifying man as an animal and explaining his origin in the same way as that of the lower creatures? If this upset our philosophy of life, we shall have to reconstruct our philosophy of life, and that would be a better task for Mr. Bryan and other spiritual teachers, than discrediting and misrepresenting established truth and maligning a great group of conscientious and devoted scientists who are consecrating their lives to search after the knowledge of nature which is constantly adding to the happiness and well being of the human race.

Mr. Bryan next makes the statement that natural selection is being increasingly discarded by scientists. In this he displays lamentable ignorance of the facts and is evidently misled by the ignorant or sophistical authorities upon whom he relies. The truth is that natural selection is not a theory but a fact. Not only is it accepted as such by all scientists, but also by all men who think about it at all. We see its operation around us every day. It involves the struggle for existence and the survival of the fittest. That is what natural selection is. We see this struggle and survival among men, in business, at the bar, in the teaching profession. Many fail and the ablest find their way to the top. This is selection and it is natural, hence, natural selection. We see it in the plants that grow upon our lawns. They are crowded, they contend, or struggle for light, for water, for room, for food; the strongest, or best adapted, or fittest, win in the fight and succeed in reproducing their kind; the weak, the less adapted, succumb and are weeded out. Among animals the same law holds good. The race is to the swift and the battle to the strong. No, natural selection is not being discarded, it is a fact, a law of life.

It is true that some biologists do not regard natural selection as the sole or even chief factor in evolution, but all are agreed that it is at least one of the factors. Darwin’s theory of the origin of species was based upon natural selection as the prime factor in evolution. Discoveries since Darwin’s day have brought to light other possible factors, hence the discussion and disagreement among the doctors; not upon the fact of evolution but upon the factors, or causes, or methods, or details in individual cases. It is upon the failure to recognize this point that Mr. Bryan is unwillingly led into his absurd blunder.

Mr. Bryan next undertakes to refute the theory of evolution by stating four objections, as follows:

1. That it is a hypothesis;
2. That it is not supported by the Bible;
3. That it is not supported by the facts;
4. That some of its explanations are absurd.

Let us examine these objections in order: Number one, that it is a hypothesis or theory. Mr. Bryan is hardly fair on this point. He says that a hypothesis is merely a “guess” and ridicules the idea of basing so important a thing as the origin and destiny of man on a mere guess. This is not argument; it is a trick of the orator to amuse or mislead his auditors and should not be allowed in the discussion of a serious question.

There is no inherent objection to a hypothesis. It is a tentative explanation. It is not formed without reason, but it is based upon known facts. It must conform to these facts. If it be a correct hypothesis, newly discovered facts must conform to it. Otherwise, a new hypothesis must be made. Mr. Bryan, no doubt in his law practice, has found it necessary to form hypotheses and to develop his cases in conformity with them. Darwin observed and studied and recorded the facts of nature for over 20 years—the diversity of species, the distribution of plants and animals on the surface of the earth, the occurrence of fossils in the bowels of the earth, the grouping of animals into classes or families, the origin of domestic races of plants and animals and a thousand other facts—and, in seeking for an explanation for these facts, formulated his hypothesis of evolution. Of course, there were difficulties in explaining all the multitude of facts by his hypothesis, because many of them were imperfectly known, but the great majority fell into his scheme and, since his day, the thousands of other facts discovered have only served to strengthen and confirm the hypothesis; until now there is no longer any doubt and the hypothesis has passed into a law. At first the sphericity of the earth was a hypothesis. It was an explanation of certain facts. After discovered facts conformed to the hypothesis, we now do not think of it as a hypothesis, but as a fact.

Mr. Bryan’s second objection is that evolution is not supported by the Bible. Neither is the atomic theory nor the theory of electrical conductivity supported by the Bible. No modern scientist would think of appealing to the Bible in support of his theory. Imagine Einstein appealing to the Bible in support of his theory of relativity! How far would he get? He would only make himself a laughing-stock in the scientific world and among theologists as well. It is a prostitution of the Bible to suppose that it teaches science, or gives any scientific information.

In the third place, and this is the crux of his whole argument, he affirms that “neither Darwin nor his supporters have been able to find a fact in the universe to support their hypothesis.” What can he mean by this statement? Can it be possible that Darwin and Huxley, Pasteur and Gray, Lamarck and Geoffroy Saint-Hilaire, Wallace and Romanes, Cope and Osbourne, Haeckel and Weismann and all the host of scientists of our time hold to
a theory that has not a single fact to support it.\textsuperscript{37} Whatever
may be said of scientists they are not fools and only a fool
would hold to a theory unsupported by a single fact. It is a
terrible arraignment of scientists. Would Mr. Bryan with
his limited knowledge of science deliberately maintain
such a thesis? The fact is he has been hoodwinked by the
authorities upon whom he depends for his information.

There are thousands of facts well known to biologists, all
of which support the theory of evolution. It would exceed
the limits of this paper to cite any considerable number of
these facts. I shall content myself with referring briefly to
only a few of them.

It has been observed that the animals of the past—as we
discover from their fossil remains—are different from the
animals of today. The remains of animals found in the
recent geological strata, while unlike the present-day ani­
mals, resemble them in many ways. We may not be able to
find the same species, but we do find the same genera or
families. And so the further back we go the stranger do the
forms appear. How shall we explain this well authenticated
ancestor.\textsuperscript{58} We recognize in the wolf and fox
members of the cat family; hence, we say that the fox and
and the Russians. Why? Because we know that they are
more nearly related. We do not have to go so far back to
discover their common ancestor. In like manner we know
that the English are more closely related to the Russians
than they are to the Japanese. If we did not have historical
records, we should just as certainly be able to reach these
same conclusions from an examination of physical charac­
teristics, language, customs, etc. The point is: Our classifi­
cation is based on a relationship—blood kinship. The
closer any two groups are to their common ancestor, the
more characteristics do they possess in common.

No one questions that this principle of classification for
the human race conforms to actual blood kinship—why
should it not indicate the same thing for the lower animals?
But I shall forbear citing from comparative anatomy,
comparative physiology, comparative embryology and geo­
ographical distribution, all of which contribute evidence to
the theory of evolution just as strong as the examples
already cited.

Mr. Bryan then goes on to say that "with millions of
species, the investigators have not been able to find one
single instance in which one species has changed into
another. . . . " This statement reminds Professor Conklin of
Josh Billings,\textsuperscript{59} who doubted the statement he had heard
that a toad would live 400 years. Josh said he would catch
one and see if it did. In most instances, at least, new species
have arisen so slowly that it would hardly be reasonable to
expect their detection within the brief space of a single
human life. Nevertheless, there is abundant proof that new
species have arisen, even if they have not been caught in
the act. The present species of animals are not the same as
those of the Eocene times—or those of the Eocene the
same as those of the Carboniferous, nor those of the
Carboniferous the same as those of the Silurian. Whence
the multitude of new species appearing in the successive
strata of the earth? Were they new creations through the
millions of years these strata were in forming? If so, what
becomes of the days of creation?

How would Mr. Bryan and his school of thinkers explain
the Archaeopteryx, that remarkable bird-reptile so marvel­
ously preserved in the Cretaceous limestones?\textsuperscript{60} Here we
have an animal with the teeth and claws and long verte­
brated tail of a reptile, but the beak and wings and feathers
of a bird. What is its significance if not a transitional form
between reptiles and birds? A distinct species no doubt in
its day, but clearly pointing backwards to its ancestors and
forward to its descendants.

But we are not left to such evidences as these, good as
they may be, for recent investigators have actually seen
species in the making. De Vries\textsuperscript{61} of Amsterdam has ob­
served the mutations of the evening primrose giving rise to
new species and Morgan\textsuperscript{62} of Columbia University has seen
the same thing with the Drosophila, or fruit fly.

But why heap up evidence? If Mr. Bryan can in the face
of these facts still ask "is it not more rational to believe in
creation of man by separate act of God than to believe in
evolution without a particle of evidence?" then the case is
hopeless, so far as Mr. Bryan is concerned.
After having disposed of the theory of evolution to his entire satisfaction as untrue and absurd, Mr. Bryan proceeds to a second part of his article in which he declares that "the objection to Darwinism [and by Darwinism he evidently means evolution] is that it is harmful, as well as groundless." He then proceeds to show that the effect of the acceptance of the doctrine of evolution would be to belittle the Bible, destroy religion and remove all basis for morality.

However, before closing, he makes this significant statement:

The real question is, Did God use evolution as His plan? If it could be shown that man, instead of being made in the image of God, is a development of beasts we would have to accept it, regardless of its effect, for truth is truth and must prevail. But when there is no proof we have a right to consider the effect of the acceptance of an unsupported hypothesis.

But suppose it turns out that it is not an unsupported hypothesis, as all the evidence clearly indicates. What then? Mr. Bryan's description of calamities to follow the acceptance of the doctrine must fall to the ground, "for truth is truth and must prevail."

Were it not better for Mr. Bryan and his fellow crusaders to accept evolution as God's method and spend their time and energy in adjusting worn out theological dogmas to newly discovered truth? The masses of the people, who are not able to make this adjustment for themselves, stand in need of a prophet and I know of no more fruitful field for the service of humanity at the present time than this bringing of the foundations of religious belief into conformity with scientific truth. In a recent essay Reverend Ralph Inge,64 Dean of St. Paul's, London, says:

The worst enemies of Christianity are Christians. When traditional orthodoxy provokes the moral indignation of the enlightened conscience, and when it outrages our sense of truth and honesty by demanding our assent to scientific errors which were exploded centuries ago, then indeed the church is in danger, and its well disciplined battalions will not save it from disaster.

The status of religion in the world today is a matter for deep concern. There has been and undoubtedly is at the present time in our own country a drifting away from the "old time religion" of our fathers—a breaking away from conventional orthodoxy—a tendency away from the blind acceptance of authority and towards a demand for a reasonable foundation of faith. Religious leaders of the Bryan type are rendering this situation more critical, since they present the dilemma of either closing the mind to the acceptance of new truth and blindly clinging to traditional orthodoxy or accepting truth as it is revealed by science and rejecting theological dogmas not in conformity with it.

There is no middle ground with them. It is either the "old time religion" or no religion. Evolutionists, according to them, are necessarily either atheists or agnostics.

Many eminent and devout seekers after truth both in the realms of science and religion do not agree with them, but are working in the conviction that God is one God, the same yesterday, today and forever and is consistent whether he reveals himself to man through the material universe or through the spirit, both of which are the products of his creative acts. Science and religion are both essential for man's well being and progress. Professor William Patten,65 in an address before Section F, Zoology, of the American Association for the Advancement of Science, St. Louis, January 31, 1919, well expresses this idea in the following words:

In that phase of cosmic evolution which we call social growth, science and religion are the outstanding cooperative agents. They better serve their ulterior purposes the better their mutual services, and the better their mutual adaptation of thought and act to creative ends.

Science and religion always have asked, and doubtless always will ask, the same fundamental questions. What creates, what preserves, and what destroys the products of nature, and how may man profit thereby? The answers, whatever they may be, must ultimately be expressed by them in essentially equivalent terms. . . .

Comments on Moore's Manuscript

In describing his schooling before entering South Carolina College, Moore remarked that he had received little training that encouraged him to think, but much that increased his "reverence for authority." That observation aptly describes the kind of instruction received by many young people in the United States today. "Reverence for authority" in the last third of the 19th century can be understood, if not excused, especially in South Carolina which had few schools and very limited financial resources in those decades immediately following the Civil War, but training that encourages appeal to expert sources should not be condoned today.

When reading Moore's discourse, one should keep in mind that it appears to have been written in 1929, well before the evolutionary synthesis of the 1930s and 40s, that grand marriage of the two schools of evolutionary biology. Those schools represented distinctly different research traditions, on the one hand that of the population naturalist and on the other that of the experimental geneticist (Mayr, 1982: 566-570). In view of the fact that Moore's graduate training and research interests were more in the sphere of the geneticist than in that of the naturalist, it seems remarkable, at first glance, that he grasped the importance of natural selection to the evolutionary process—something that cannot be said of many of his contemporaries. His involvement with teaching, requiring a
broad-based approach to biology, and his establishment of a botanical collection, bringing him into contact with the immense variation found in nature, no doubt led him towards an appreciation of the contributions of the naturalists and the significance of natural selection to evolution.

In his critique of William Jennings Bryan's comments on evolution, Moore examined, among other things, the objection that evolution is an hypothesis and clearly explained the nature and function of hypotheses. At present, there is still much misunderstanding among the general population as to the place of hypotheses in the domain of science, and many people would be well served by taking Moore's remarks to heart. Moore was inconsistent in referring to the doctrine of evolution, variously attributing to it the status of hypothesis or that of theory. If a theory be considered a well-corroborated hypothesis, then evolution is more appropriately regarded as a theory than as an hypothesis.

In several places Moore spoke of the concepts of evolution and natural selection as being facts. In view of the ordinary usage of the word "fact," there is no question that many evolutionary biologists of today would agree with those sentiments, but some of those of a more philosophical cast would ask "what exactly is a fact?"—not being satisfied with dictionary definitions of the word. It would have been better if Moore had treated natural selection as a theory (or well-corroborated hypothesis), leaving little room for philosophical carping.

Moore was essentially correct when he wrote about the biologists of his day that "some ... do not regard natural selection as the sole or even chief factor in evolution, but all are agreed that it is at least one of the factors." Before the evolutionary synthesis, many biologists—in fact virtually all experimental biologists—rejected natural selection, at least "as the exclusive direction-giving mechanism in evolution," but opposition was not complete, for "almost all opponents allowed for some selection but claimed that major evolutionary phenomena and processes could not be explained by it" (Mayr, 1982: 514–515, 518).

In order to illustrate the kinds of evidence evinced in support of evolution, Moore made brief and effective mention of a few easily understood examples, choosing from paleontology the phylogeny of the horse and the Jurassic bird Archaeopteryx; a wonderful transitional animal, and from taxonomy the recognition of characteristics that require the classification of the wolf, fox, and dog in the Family Canidae—the lion, tiger, leopard, and domestic cat in the Family Felidae—and those two families, together with other families, in the Order Carnivora. He demonstrated a good understanding of the significance of classification and, by implication, phylogeny.

The modern creationists have assiduously followed their predecessors of Moore's day in misunderstanding the disagreements on evolutionary theory that periodically occur among biologists. The disagreements, rather than being a sign of weakness, are strong evidence of a vigorous, healthy science—a science that has engaged the interest of many very bright minds. As noted by Moore, "The debate among modern evolutionists is not over the fact of evolution, but over its causes, its methods and its course." That statement is timeless, as true today as when it was written. Consider, as examples, the different emphases currently placed by "micro-" and "macro-" evolutionists on phenomena such as selection, genetic drift, extinction, punctuated equilibria, heterochrony, and epigenetic interactions.

Moore's treatise was (and still is) a good introduction to evolutionary biology for those having little or no scientific background. His positions as a respected faculty member at the University and as a pillar of society in Columbia probably made it easy for him to discuss evolution publicly outside the University setting, particularly before a well-educated audience, and the fact that he was a theistic evolutionist no doubt made it even easier for him to declare his point of view. In any event, Moore's presentation of his evolution paper at a meeting of the Kosmos Club was so well received that the Club devoted a second entire meeting to discussing it. It would be interesting to know how Thomas Cooper, who seemed to be continually at odds with the Presbyterians, and James Woodrow, who struggled mightily within the Presbyterian Church for his academic freedom, would have responded to the talk given by Moore, who belonged to an apparently more tolerant Presbyterian Church than the one that existed during the 19th century. The leadership of the Presbyterian Church in the South may have learned from the embarrassment accompanying the Woodrow War and as a consequence become more forbearing during the 1920s (Numbers and Stephens, 1998: 73–74).

Discussion

The history of the conflict between the advocates of evolution and the proponents of creationism points out in microcosm two much larger issues—inequitable understanding in the United States of what is meant by academic freedom and the boundless ignorance of the average American in the realm of science. Although academic freedom allows one to pursue and proclaim truth freely, it does not give license to expound authoritatively upon subjects outside the specialized knowledge of the speaker, a point lost to some creationists. The advocates of "creation science" have certainly exploited the lack of scientific sophistication rampant in the United States. Nevertheless, it would be misleading to view modern-day creationists as marginal to contemporary secular society because they have benefited from the spread of mass education.
Almost all claim bachelor's degrees, an estimated 40–60 per cent in some scientific or technical field. Around 10–25 per cent are trained in applied areas, particularly engineering, 20–30 per cent in physical science; and a few (5–10 per cent) in the life sciences, the most relevant for an anti-Darwinian movement. ... Many claim PhDs from accredited schools, even major universities (Cavanaugh, 1985: 185).

Mass education produces a mixed blessing, however, because it is an "oddly uneven education. It enlarges society's pool of intellectuals, but also confers academic degrees upon people contemptuous of intellect and unfamiliar with the life of the mind" (Cavanaugh, 1985: 185). But it is not to numbers that the creationists owe their successes. According to a 1985 report, the creationist movement's core of adherents is small, and its kernel (actual members of scientific creationist organizations) numbers no more than several thousand worldwide. The movement's influence increases "within an opportunity structure whereby (1) the core uses (2) a protective belt of mainstream intellectuals (willing and unwilling) plus (3) the contemporary climate of public opinion and scientific understanding" (Cavanaugh, 1985: 188).

In a nation that values anti-intellectualism and religious extremism more than scientific literacy, the scientific community has its work cut out for it in the continuing, but poorly recognized, conflict with the creationists. If nothing else, the creationists are relentless. In April 1994, the school board in Tangipahoa Parish, Louisiana, passed a requirement that whenever the scientific theory of evolution is to be presented, a disclaimer must be read, informing students that the material "should be presented to inform students of the scientific concept and not intended to influence or dissuade the Biblical version of creation or any other concept." Such disclaimers, which are probably unconstitutional, make evolution appear shaky (Futuyma, 1995: 251).

Reading about events such as the nearly successful attempt by creationists to take over a school board in Fairfax County, Virginia, in suburban Washington, D.C.; the effort by officials of the City of Tulsa, Oklahoma, to remove exhibits on the evolution of the horse from the local zoo; and an attempt by a high-school student in Jefferson County, Colorado, that almost succeeded in having a "Nova" film "banned from the biology classes ... because it mentioned in passing that all living things are descended from a single cell" (Storey, 1997: 68), it becomes clear that in some engagements common sense has prevailed, but the struggle is far from over.

That it is not over was made abundantly clear in the decision by the Kansas State Board of Education on 11 August 1999 to adopt a "compromised set of Science Education Standards," empowering each of the 304 school districts in the State to decide whether to teach evolution in science classes. The Board of Education's Standards do not prevent teaching evolution in public schools, but, because the Standards will be used to establish the content of assessment examinations required in the sciences, it is feared that teachers will spend less time on evolution and more on subject areas that will be included on tests. Another concern is that the decision will lead to pressure to introduce "creation science" into the curriculum (Cunningham, 1999: 10). Less well known than the controversy in Kansas are rumblings of discord emanating from Idaho and Colorado. At least one anti-evolutionary text has been submitted to the Idaho Department of Education for consideration for adoption as a text in biology, and it has been reported that anti-evolutionists, in pursuit of their goals, have been meeting actively with a number of individuals in the Idaho Department of Education. Interestingly, Idaho, as this is being written, is developing exit standards for high school students (Bennett, 1999). In the spring of 2000, eighth-grade students in Colorado will, for the first time, take a statewide science test, but there will be no questions on human evolution because state standards don't specifically require schools to cover that area of biology. Human evolution was intentionally left out when the standards were written in 1995 because some individuals involved in their development were "opposed to giving more credence to evolution than 'creation science'" (Petto, 1999: 23).

If the creationist movement flourish "on an outmoded philosophy of science," as has been suggested, perhaps "including the history, philosophy, and sociology of science as an integral part of science education might" contribute significantly to shrinking the protective belt of mainstream intellectuals to whom the movement can appeal (Cavanaugh, 1985: 189).

Conclusion

If the general public could learn what science is and to recognize the features that distinguish it from pseudoscience, the creationist movement would eventually go the way of the dinosaur. In a short essay published in American Scientist, Edward O. Wilson offered a succinct definition of science and a brief discussion of its diagnostic characteristics. He considers science to be "the organized systematic enterprise that gathers knowledge about the world and condenses the knowledge into testable laws and principles" and its distinctive aspects to be repeatability, economy, mensuration, heuristics, and consilience. Wilson maintained that astronomy, biomedicine, and physiological psychology have all of these features, but astrology, ufology, "creation science," and Christian Science have none of them (Wilson, 1998b: 6).

During the 1980s and 90s, a number of legal encounters
with creationists were fought and won by evolutionists. In spite of those victories, the contest may very well be lost if people do not become aware of what is at stake. Stemming the tide of misinformation that threatens to control public opinion is an enormous task that needs immediate attention. The seriousness of the situation was well stated in the Op-Ed section of the New York Times by Lawrence Krauss, Chairman of the Department of Physics, Case Western Reserve University, when he wrote:

Nonsense masquerading as truth has been with us as long as records can date. But the increasingly blatant nature of the nonsense uttered with impunity in public discourse is chilling. Our democratic society is imperiled as much by this as any other single threat, regardless of whether the origins of the nonsense are religious fanaticism, simple ignorance or personal gain (Krauss, 1998: A19).

Rather than continuing to counter the guerrilla-warfare harassment of the creationists, rebutting individual arguments as they arise, it has been suggested that scientists take the offensive and "demand that creationists defend their total view of the geologic record and all their implausible and commonly ludicrous 'scientific' interpretations" (Wise, 1998: 160). There is little doubt that the same strategy could be employed profitably to oppose the entire range of claims put forth by the antievolutionists.

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Notes

1 As presented in Bartlett (1980: 596): “Reply to Wilberforce’s question,” from Leonard Huxley, Life and Letters of Thomas Henry Huxley, 1900, vol. I. Wilberforce’s question as given in Bartlett (1980: 596, footnote) is: “If anyone were to be willing to trace his descent through an ape as his grandfather, would he be willing to trace his descent similarly on the side of his grandmother?” Many years later, when recalling his immediate response to Wilberforce’s inquiry, Huxley reported that he said in an undertone to a man sitting near him, “The Lord hath delivered him into mine hands....” (Jensen, 1988: 167).

Samuel Wilberforce (1805–1873), Anglican prelate, educator, and staunch anti-Darwinian, was Bishop of Oxford at the time of his exchange with T. H. Huxley on 30 June 1860 during the meeting of the British Association for the Advancement of Science. Although there were many people (reports varied from 400 to 1,000) in the audience at the time, not one of them thought to take down either Wilberforce’s query or Huxley’s retort. The available accounts were written from memory—several hours to many years later. Consequently, we shall never know exactly what either man said. Fortunately, although differing in many details, the reports are in good agreement on the sense of the exchange (Hardin, 1961: 92–96; Meacham, 1970: 215–217; Jensen, 1988; Desmond, 1997: 276–281). As can be seen in Bernard Cohen’s comments (Cohen, 1985: 598–603) in The Darwinian Heritage, Wilberforce’s understanding of the Darwinian concept of natural selection was much better than one might assume from the question that he posed to Huxley.

The experience with Wilberforce at the meeting in 1860 changed Huxley’s opinion as to the value of public
speaking and led to his cultivating that activity. "Huxley's determination to engage in public debate on the subject of evolution—to become Darwin's bulldog—was therefore a direct consequence of his encounter with Wilberforce" (Meacham, 1970: 216-217).

2 Higher Criticism is "the critical study of the literary methods and sources used by the authors" of the Biblical texts, as distinguished from Textual (or Lower) Criticism, "which is concerned solely with the recovery of the text of the Books [of the Bible] as it left their authors' hands" (The Oxford Dictionary of the Christian Church, 1997, 3rd edition, p. 769). By 1990, the liberals (or modernists) in American Protestant denominations had accepted the scholarly methods of Biblical criticism, employed first in universities and seminaries and viewed as an important instrument for improving Christianity. Biblical criticism produced more accurate translations of religious texts and "represented another attempt to assimilate American religion into an increasingly secular community marked by a scientific outlook" (Webb, 1994: 54).

3 News and Observer, Sunday 2 May 1926, p. 3 (Raleigh, North Carolina).

4 In January 1982, Federal Judge William R. Overton (1939-2000, 2000) of Little Rock ruled that the Arkansas law was unconstitutional, and, in January 1985, Federal Judge Adrian G. Duplantier (b. 1929) of New Orleans made a similar declaration for the Louisiana law. On 8 July 1985, the Fifth Circuit court of Appeals upheld Judge Duplantier's decision and in December denied a petition for a rehearing. The United States Supreme Court agreed to hear the Louisiana case and on 19 June 1987 rendered its judgment, finding by a vote of seven to two that the law was unconstitutional (Berra, 1990: 153-158; Numbers, 1992: 249-250; Webb, 1994: 228-252).

5 A good explanation of "creation science" (or "scientific creationism") was included in the "1981 Arkansas law mandating 'balanced treatment' in teaching creation and evolution." (Numbers, 1992: 245). The Arkansas law provided the following definition:

"Creation-science includes the scientific evidences and related inferences that indicate: (1) Sudden creation of the universe, energy, and life from nothing; (2) The insufficiency of mutation and natural selection in bringing about development of all living kinds from a single organism; (3) Changes only within fixed limits of originally created kinds of plants and animals; (4) Separate ancestry for man and apes; (5) Explanation of the earth's geology by catastrophism, including the occurrence of a worldwide flood; and (6) A relatively recent inception of the earth and living kinds (Numbers, 1992: x, 245).

6 The data cited by Berra (1990: 125) were gleaned from Fuehrer (1984) and Zimmerman (1987, 1988).

7 The crisis in education in the United States is not limited to the sciences. Disturbing statistics were presented in a forum on the teaching of American history that appeared in the Winter 1998 issue of The American Scholar. "In 1995, the National Assessment of Educational Progress reported that 57 percent of high school seniors scored 'below basic' in their knowledge of American history. It is not possible to score any lower than that." According to a report on "America's Teachers" released by the U. S. Department of Education in mid-1997, 59 percent of the nation's social studies teachers lack a major or minor in an appropriate subject area. "This means that a majority of those who teach social studies have studied few if any courses in history, political science, economics, sociology, or any other social science." And it is even worse for middle and high schools, where 82 percent of social studies teachers do not have a major or a minor in history (Ravitch, 1998: 104). There is little sign of relief on the horizon.

History departments in colleges and universities in the United States have suffered dramatic losses in students in recent years. After reaching a peak of 44,663 in 1971, the number of bachelor's degrees awarded in history dropped precipitously to 16,413 in 1986, although total enrollments in colleges were increasing rapidly, making the drop in percentage of degrees granted in history even more striking—from 5.3 to 1.7 percent of the total. "By 1990 students could graduate from some 78 percent of American colleges without taking a course in the history of Western civilization." There have been some signs of improvement in the status of history in academia during the last ten years, but "full recovery still seems remote" (Woodward, 1998: 105-106).

Considering the overall quality of the training of those teaching in American public schools, it is more surprising that many of their students do extremely well academically than it is that large numbers of them learn almost nothing at all.

8 One writer described Thomas Cooper as "the Unitarian radical" and as "a somewhat cranky British Unitarian" (May, 1976: 219, 333). Another, who wrote on Cooper's public life, noted that "he gave nominal adherence to Unitarianism as the most rational and comprehensible theological system" and that he held a higher opinion of Unitarians than of the members of any other religious assemblage (Malone, 1961: 17, 262), but Daniel W. Holis, author a history of the University of South Carolina, referred to Cooper as a Deist (Hollis, 1951: 107). Whether one would prefer calling him a Unitarian or calling him a Deist, Cooper's outlook on religion veered far from orthodox Christianity.

There seems to be a long-standing tradition of defining Unitarianism by what it isn't rather than what it is. The name itself seems to suggest that denials of the deity of Christ and the doctrine of the Trinity are the most dominant tenets of this religion, but "the stress on moral culture and the corresponding rejection of innate depravity were the defining impulses of that tradition" (Robinson, 1985: 29). Robinson (1985: 121) quoted what "has been recognized...as one of the most moving and accurate statements of faith among Unitarians,..." That statement does not dwell on negatives; instead, it is a very positive declaration.

Unitarianism developed in separate movements in Poland, Transylvania, England, and the United States, primarily as a result of factors peculiar to each region. The various Unitarian movements had a number of characteristics in common: "affirmations of the unity of God, the humanity of Jesus, and human religious responsibility, and rejections of the doctrines of the Trinity, the divinity of Jesus, and human
corruption or total depravity. Formulations of these views differed in each country" (Godfrey, 1987: 143-144).

Among the individuals having an important influence on the development of Unitarianism in the United States was Joseph Priestley (1733-1804), chemist, physicist, clergyman, educator, and political theorist, who was born and spent most of his life in England, immigrating to America in 1794, after having become controversial because of his religious views and his sympathy for the French Revolution (Robinson, 1985: 21-23, 309-310). Thomas Cooper became well acquainted with Priestley in England and developed a very close relationship with him after both men settled with their families in Northumberland, Pennsylvania (Malone, 1961: 79-83).

During the 19th century, Unitarians had an influence on the intellectual life of the United States that far surpassed what might have been expected from their relatively small numbers. A listing of important 19th-century American Unitarians would include the poets William Cullen Bryant (1794-1878) and Henry Wadsworth Longfellow (1807-1882), the essayist, poet Ralph Waldo Emerson (1803-1882), and the historian Jared Sparks (1789-1866) (Beattie, 1985: 688; Robinson, 1985: 252-253).

Seemingly even further afield from conventional Christian theology than Unitarianism, Deism, also known as the Religion of Nature or natural religion, "is the view that the existence of a superior being or first cause may be demonstrated by human reason independently of any kind of supernatural revelation" or the teaching of any church. There are, however, a number of variations on this concept, ranging from militant anti-Christian Deism to Christian Deism (Aldridge, 1985: 134). For all practical purposes, a Deist is an individual living in a Christian culture who refers to belief in God without belief in supernatural revelation, or the teaching of any church, and also a Deist (Aldridge, 1985: 134). Even Jefferson, an agnostic (Greene, 1981: 137). By about 1860, Darwin, his codiscoverer of the principle of natural selection Alfred Russel Wallace (1822-1913), the biologist Thomas Henry Huxley (1825-1895), and the philosopher Herbert Spencer (1820-1903) had "reached similar views concerning nature, man, God, history, society, and science..." (Greene, 1981: 148).

In view of his friendship with Joseph Priestley, it is not surprising that Thomas Cooper has been considered by some to have been a Unitarian. In addition, there is disagreement among authors as to the religious persuasion of others of Cooper's day. As examples, Thomas Jefferson, usually considered a Deist, is in at least one source called a Unitarian (Beattie, 1985: 688), and John Adams has been termed a Unitarian (May, 1976: 280; Beattie, 1985: 688) and also a Deist (Aldridge, 1985: 137). Even Jefferson, an admirer of Joseph Priestley, was not always sure of his position, sometimes thinking of himself as a Unitarian rather than as a Deist (May, 1976: 293). Such confusion is probably in large extent due to the fact that in the United States Deism and Unitarianism held much in common during the last half of the 18th century and the early part of the 19th century, and as the Deistic movement died out some of the Deists found a home with the Unitarians. Neither group had a creed and both relied on reason for religious insight, but Unitarians were organized with ministers, church buildings, and congregational governance, whereas Deists lacked a formal religion (Wright, 1976: 3-8; Aldridge, 1985: 134, 137; Beattie, 1985: 679-688; Robinson, 1985). If it be possible to pigeonhole Cooper's religious philosophy into a distinct category, it would seem to fit better with Deism than with Unitarianism, though perhaps not as comfortably as one might wish.

9 Thomas Cooper's unorthodox outlook on religion did not endow him with exclusive or special credentials to discredit the Mosaic account of creation. There were a number of other geologists, contemporary with Cooper, who did not subscribe to the Mosaic account. That group included

Among the American Deists of that day were the jack-of-all-trades Benjamin Franklin (1706-1790), the first and third presidents of the United States, George Washington (1732-1799) and Thomas Jefferson (1743-1826), the revolutionary author and agitator Thomas Paine (1737-1809), the soldier and author Ethan Allen (1737-1789), and the poet Philip Freneau (1752-1832) (Dictionary of American Biography, 1964, Vol. 1, Part 1, p. 188; 1962, Vol. 7, Part 2, p. 159; May, 1976: 236-239, 326; Greene, 1984; 12; Schwartz, 1987: 174-177), John Adams (1735-1826), the second president of the Republic, was a freethinker, disinclined to accept authority or dogma, hence little removed from Jefferson in religious beliefs (Koch, 1964: 269, 284) and sounding at times "almost exactly like Franklin" (May, 1976: 280). Deism was an essential component of the effort by such men to "rationalize human institutions in behalf of liberty and progress" (Greene, 1984: 13).

Interestingly, Charles Robert Darwin (1809-1882) in his religious trek from Biblical literalist, as a young man, to agnostic, in his later years, passed through a period in which he was a Deist (Greene, 1959: 354-337; Bowler, 1990: 41, 84-85, 207). In fact, he was still a Deist in 1859, the year the Origin of Species was published (Greene, 1981: 137). By about 1860, Darwin, his codiscoverer of the principle of natural selection Alfred Russel Wallace (1822-1913), the biologist Thomas Henry Huxley (1825-1895), and the philosopher Herbert Spencer (1820-1903) had "reached similar views concerning nature, man, God, history, society, and science..." (Greene, 1981: 148).

10 In his earlier writing Thomas Cooper had "denied the existence of the human soul, freedom of will, eternal duration of future punishments, and the doctrine of the Trinity" (Hollis, 1951: 98-99; Malone, 1961: 270). Dumas Malone (1961), in his biography of Cooper's public life, vividly described much of the controversy that seemed to be the constant companion of this extraordinary man. Although Cooper's conflict with organized religion, particularly that with the Presbyterians, pervades much of Malone's book, a chapter entitled "The President and the Priesthood, 1829-1839" is particularly useful in understanding the nature of the dispute.


12 John Calvin (christened Jean Cauvin) (1509-1564) was a French theologian, Biblical scholar, church organizer, and one of the most important leaders of the Protestant Reformation of the 16th century. He was also a humanist and linguist, assisting in shaping and standardizing French language and literary style. Calvin spent a large part of his life in Geneva, where he used his great intellect, his organizational talents, and his considerable abilities as a leader to influence the development and spread of Protestantism, his efforts ultimately having a prodigious impact on the religious history of the West. The representative form of church government developed by Calvin has had an important influence in the development of the democratic political structures of the Western world. (Armstrong, 1987: 31-54). Theology of the Reformed and Presbyterian churches is based on Calvinism.

13 The D. H. Chamberlain with whom Woodrow corresponded was apparently Daniel Henry Chamberlain (1835-1907), who served as Republican Governor of South Carolina from 1874 to 1876. After an extremely bitter campaign, Chamberlain was apparently reelected in November 1876, but the Democrats challenged the election. The matter was not settled until April 1877 when President Rutherford B. Hayes (1822-1893) withdrew Federal troops, ending Reconstruction in South Carolina. Without the support of the troops, Chamberlain had no power and was forced out of office, allowing Wade Hampton (1818-1902) to assume the governorship. (Dictionary of American Biography, 1957, Vol. 2, Part 1, p. 595; Sobel and Raimo, 1978: 1418).

14 Papers of James Woodrow, microfilm roll no. 128, Manuscript Division, South Caroliniana Library, University of South Carolina, Columbia. Also see Chamberlain, 1891: 551.

15 "Aside from his support of evolution, he [Thomas Howard MacQueary] also voiced the opinion that there was not a bodily resurrection [of Christ]. He was put on trial for heresy and defrocked in 1891. He went from here [Ohio] to a Universalist church in Saginaw, Michigan" (personal communication from Donald J. Sheppard, 30 March 1998). In a subsequent communication (11 April 1998), Sheppard wrote, "By the way, it turns out that MacQueary was not deposed but was suspended and then renounced his vows. It was later found that the court did not have the authority to depose him." According to Albright (1964: 311) and Prichard (1991: 186), MacQueary was convicted of heresy for denying the doctrine of the Virgin Birth of Christ.

MacQueary (1861-1930 [1931?]) was very well educated, graduating from the Theological Seminary of the Protestant Episcopal Church (Alexandria, Virginia) in 1886, taking his A. M. degree from the University of Minnesota in 1898, and completing work for his Ph. D. degree at the University of Chicago in 1901. After serving as an independent minister in Saginaw, Erie (Pennsylvania), and Minneapolis, MacQueary worked as a teacher and school administrator in Chicago and St. Louis and lectured before Chautauqua assemblies and other groups (The National Cyclopaedia of American Biography, 1929, Vol. VI, p. 299; Who Was Who, 1942, Vol. I [1897-1942], p. 766; Jansen, 1965: 84).

16 Interestingly, the MacQueary case was not the only instance of a trial for heresy in the North during the 19th century and the early years of the 20th century. George Shriver (1966) edited a volume covering five of the major heresy trials in American Protestant Christianity that occurred in the period 1845 to 1906. Of those five, four concerned heresy in northern churches—German Reformed (Mercersburg, Pennsylvania), Presbyterian, U. S. A. (New York City), Methodist Episcopal (Boston), and Protestant Episcopal (Rochester, New York); the fifth involved the Southern Baptist Church (Louisville).

17 John Merle Coulter (1851-1928) was a botany professor at the University of Chicago (1896-1925), where he built up a strong department in teaching and research. He founded the Botanical Gazette in 1875, while serving on the faculty of Hanover College (Hanover, Indiana), wrote numerous textbooks and manuals of botany, penned a number of taxonomic monographs and shorter contributions, and was extremely influential through the excellent training that he provided his students (Dictionary of American Biography, 1958, Vol. II, Part 2, pp. 467-468).

18 From typescript of "Evolution Once More" by Andrew Charles Moore; Papers of Andrew Charles Moore, Manuscript Division, South Caroliniana Library, University of South Carolina, Columbia.

19 Papers of Andrew Charles Moore, Manuscript Division, South Caroliniana Library, University of South Carolina, Columbia. The Mr. Bryan mentioned here was William Jennings Bryan (see Note 50).

20 "In Memoriam [to] Andrew Charles Moore, 1866-1928," (p. 26) by George Armstrong Wauchope, Professor of English, University of South Carolina. The "In Memoriam" is undated, but was presumably printed and distributed in late 1928 or early 1929 because it includes the program for
"Memorial Exercises" that were held in the University Chapel on 30 October (apparently 1928).

Moore served from 1902 until his death as a member of Columbia's Board of School Commissioners and was its chairman after 1906 ("In Memoriam [to] Andrew Charles Moore, 1866-1928," [pp. 24-25] by George Armstrong Wauchope; see Note 20). Fittingly, an elementary school in Columbia bears Moore's name. David H. Rembert, Jr., informed (personal communication, 4 August 1997) that, in addition to the Herbarium, a residence hall and a garden on the Columbia campus of the University have also been named for Moore.


"In Memoriam [to] Andrew Charles Moore, 1866-1928," (p. 25) by George Armstrong Wauchope (see Note 20).

Papers of Andrew Charles Moore, Manuscript Division, South Caroliniana Library, University of South Carolina, Columbia.

The typescript is in the Papers of Andrew Charles Moore, Manuscript Division, South Caroliniana Library, University of South Carolina, Columbia.

The "War" mentioned here was the American Civil War, or War Between the States, 1861 to 1865.

The institution called South Carolina College in Moore's undergraduate days became the University of South Carolina in 1906 (Hollis, 1956: 197).

Dr. Woodrow was James Woodrow, discussed at length earlier in this paper. The address mentioned here is the one Woodrow gave before the Alumni Association of the Columbia Theological Seminary on 7 May 1884. Excerpts from that address are presented herein in the section on Woodrow.

Andrew Dickson White (1896, vol. I: 9) in remarking upon the date of creation wrote:

Suffice it here that the general conclusion arrived at by an overwhelming majority of the most competent students of the biblical accounts was that the date of creation was, in round numbers, four thousand years before our era; and in the nineteenth century, in his great work, Dr. John Lightfoot, Vice-Chancellor of Trinity College-Dublin, one of the most eminent Hebrew scholars of his time, declared, as the result of his most profound and exhaustive study of the Scriptures, that "heaven and earth, centre and circumference, were created all together, in the same instant, and clouds full of water, and that this work took place and man was created by the Trinity on October 23, 4004 B.C., at nine o'clock in the morning."

In the presence of such exactitude, one is tempted to ask if the good Dr. Lightfoot (1602-1675) meant 9:00 A.M. Greenwich time.

Of the many attempts to date the time of creation, one effort, cited frequently, notably in textbooks of historical geology, is that of James Ussher (1581-1656), Archbishop of Armagh, Vice-Chancellor of Trinity College—Dublin, Biblical scholar, and expert on Semitic languages. In a volume published in 1650, Ussher indirectly indicated the time of creation as Saturday evening 22 October 4004 B.C. He apparently used both the timing of events in the Old Testament and astronomical cycles to make this very precise determination (Brice, 1982: 18-20; Bailey, 1993: 200).

John Lightfoot, in a 1642 publication, did give the hour of creation of man as nine o'clock in the morning (Brice, 1982: 19), but the year 4004 B.C., attributed to him in the same quotation (White, 1896, vol. I: 9, see above), is at variance with the Lightfoot date given in another source. In a volume published in 1644 Lightfoot declared 3928 B.C. to have been the year of creation (Brice, 1982: 19).

Moore's statement that "the doctrine of uniformitarianism" was "first clearly promulgated by the great English geologist Lyell" is in error. That doctrine, initially formulated by the Scottish geologist James Hutton (1726-1797), was published in the latter part of the 18th century, but Hutton's style of writing was difficult to read, and his work might have been neglected had it not been for the efforts of his friend John Playfair (1748-1819), another Scotsman. Fortunately, Playfair (geologist, mathematician, and minister) clearly explained and expanded on the concepts of uniformitarianism, publishing a treatise that popularized Hutton's work (see Note 9) (Dictionary of Scientific Biography, 1972, Vol. 6: 577-589; 1975, Vol. 11: 94-96; Gillispie, 1996: 44, 73-97).

Playfair was neither unoriginal nor uncritical, and he was more than a popularizer. He was Hutton's Huxley (see Note 32), and, like Huxley, his own contributions have been submerged in his advocacy of a larger cause (Gillispie, 1996: 74).

Moore was correct, however, in noting the importance of Lyell in disseminating the principles of uniformitarianism, and Mayr (1982: 375) wrote that "Lyell was the great champion of uniformitarianism. ..." Some of the values given here are inaccurate (e.g., the length of the main course of the Mississippi River is considerably greater than 1,500 miles; it is about 2,550 miles in length), but the discrepancies are in no instance great enough to affect Moore's argument.

William Evart Gladstone (1809-1898) was an influential leader of the Liberal Party and four times prime minister (1868-1874, 1880-1885, 1886, 1892-1894) of Great Britain. In addition to his political activities, he wrote a number of scholarly works and read very widely, becoming particularly well versed in classical studies, theology, and Italian poetry (The Dictionary of National Biography, 1937-1938, Vol. 22, Supplement, pp. 705-754; Jenkins, 1997).

Thomas Henry Huxley (1825-1895) contributed significantly to morphology, embryology, paleontology, taxonomy, physiology, and ecology and wrote several important textbooks of science (Mayr, 1982: 510; di Gregorio, 1984: 188; Bowler, 1990: 144-145). This extraordinarily perceptive man seems to have been the first to come up with the hypothesis that birds descended from theropod dinosaurs (Huxley, 1870; Desmond, 1997: 355-360; Padian and Chiappe, 1997: 72-73). After the publication of the Origin of Species in 1859, Huxley, known as "Darwin's bulldog" (see Note 1) became the chief public proponent of Darwinism. Although a strong defender of natural selection, a case can be made for his never having been a convinced believer in the theory he guarded. In fact Huxley maintained the opinion "that major saltations could achieve what gradual evolution by selection could not" (Mayr, 1982: 510-511). One historian of science has called him a "pseudo-Darwinist"
who was really interested in evolutionism—not the theory of natural selection—and who leaned towards an evolutionary model that was more dependent on non-Darwinian factors than on selection (Bowler, 1990: 142–151). Huxley had considerable impact on education, particularly in modernizing the curriculum (di Gregorio, 1984: 189, 197). "There can be no doubt that Huxley's success in promoting scientific education, through his textbooks, speeches, committee activities, and educational appointments, is one of the last monuments of his life..." (di Gregorio, 1984: 189).

Greatly interested in theology and needing a word to express his own attitude towards religion, Huxley coined the term "agnostic." In a series of articles appearing in The Nineteenth Century, he (Huxley, 1889a,b,c) discussed his philosophy and in one of them (Huxley, 1889a: 182–184) related the events that led to his inventing the new word. I have not found the exact comments attributed by Moore to Gladstone and Huxley, but I can assert with certainty that they are fully within the spirit of the controversy between those two men of erudition that warmed the pages of The Nineteenth Century in a series of exchanges that appeared in the mid-1880s. Stephen Jay Gould captured the flavor of their dispute in a chapter entitled "Genesis and Geology" in his Bully for Bronislaus (Gould, 1991: 402–415). In reading the articles in The Nineteenth Century it is easier for me to identify the position taken by Huxley than that of Gladstone, perhaps because Huxley was more accustomed than Gladstone to writing on scientific subjects. The following remarks could lead one to consider Gladstone to have been to some degree, at least, a theistic evolutionist.

Not that I share the horror with which some men of science appear to contemplate a multitude of what they term 'sudden' acts of creation. All things considered, a singular expression: but one, I suppose, meaning the act which produces, in the region of nature, something not related by an unbroken succession of measured and equal stages to what has gone before it. But what has equality or brevity of stage to do with the question how far the act is creative? I fail to see, or indeed am somewhat disposed to deny, that the short stage is less creative than the long, the single than the manifold, the equal than the jointed or graduated stage. Evolution is, to me, series with development. And like series in mathematics, whether arithmetical or geometrical, it establishes in things an unbroken progression; it places each thing (if only it stand the test of ability to live) in a distinct relation to every other thing, and makes each witness to all that have preceded it, a prophecy of all that are to follow it (Gladstone, 1886: 18).

In an article entitled "Science and pseudo-science," in response to a contribution by the Duke of Argyll (1887) that was highly critical of Huxley's comments on a sermon by a prominent clergyman, Huxley (1887: 490) wrote that "creation 'operating by law' is constantly cited as relieving the Creator from trouble about insignificant details." That quotation smacks of the declaration ascribed by Moore to Gladstone.

George Douglas Campbell, eighth Duke of Argyll (1823–1900), became a member of the House of Lords in 1847 upon the death of his father. A talented man—statesman, writer, and orator—possessing an interest in science, particularly in geology and ornithology (The Dictionary of National Biography, 1957–1958, Vol. 22, Supplement, pp. 385–391), Argyll was an advocate of theistic evolution and author of The Reign of Law (1866) in which he "invoked the beauty of species such as the hummingbirds as evidence that the Creator intended evolution to have more than purely utilitarian purposes" (Bowler, 1990: 166, 206). Huxley obviously enjoyed the exchanges that he had with the Duke, as can be seen from the following excerpt from a letter to the editor of Nature (Huxley, 1888: 342):

The Duke of Argyll's singular appetite for bemirching the characters of men of science appears to grow by what it feeds on; and, as fast as old misrepresentations are refuted, new ones are evolved out of the inexhaustible inaccuracy of his Grace's imagination.

33 George Dod Armstrong (1813–1899) was "the leading spokesman on science and religion among Southern Presbyterians in the late nineteenth century. ..." An alumnus of Princeton, he taught chemistry and geology for 13 years at Washington College in Lexington, Virginia, before becoming the pastor of the First Presbyterian Church in Norfolk (Numbers, 1992: 12). (Washington College became Washington and Lee University in 1871 (Senge, 1978: 296).)

34 John Christian Keener (1819–1906), minister in the Methodist Episcopal Church, South, served as a bishop for 28 years, becoming "one who typified the arbitrary attitude that often marked the bishops of his day" (The Encyclopedia of World Methodism, 1974, Vol. 1, p. 1318).


Moody was very clear in describing the kind of people he hoped to train at his Institute for missionary work. "We want men who can do something uncommon. Any man can eat soup with a spoon, but the man who can eat it with a one-tined fork is a marvel" (Chicago Tribune, 27 September 1889—as quoted by Findlay, 1969:350).

36 Alexander Patterson was a Presbyterian evangelist whose "career remains obscure," but he is known to have been a long-time friend of Dwight L. Moody's and to have been associated with the Moody Bible Institute (Numbers, 1992: 16, 354–355; see Note 35).

37 Q. E, and D are the initial letters of the words in the Latin expression quod erat demonstrandum (=which was to be demonstrated). Mathematical proofs are sometimes followed by "Q. E. D."

38 When he began his literary career, Price (1870–1963), whose original name was George Edward Price, replaced his middle name with his mother's maiden name and became George McCready Price (Numbers, 1992: 73). Price was not as well educated as one might assume upon seeing the "M. A." succeeding his name. The College of Medical Evangelists (Loma Linda, California), where Price had an academic appointment from 1907 to 1912, "awarded him a B. A. in 1912, based in part on his 'Authorship' and independent
study.... And during the last forty-five years of his life, he often tacked an M. A. onto his name, a gift from the Adventist Pacific Union College of Angwin, California (Numbers, 1992: 30, 372).

In 1906, Price sent out hundreds of complimentary copies of one of his books, *Ilogical Geology; many of these were sent to scientists with the request that they provide comments and criticisms. David Starr Jordan (1851-1931), President of Stanford University and world-renowned zoologist, provided "by far the most candid and thoughtful" response. "Off and on for almost 20 years, Jordan worked hard to get Price to see that his case against geology was "based on scattering mistakes, omissions and exceptions against general truths that anybody familiar with the facts in a general way can not possibly dispute." Impressed by his correspondent's obvious intelligence and lawyerlike mind, as well as by his ignorance of geology, Jordan repeatedly but unsuccessfully urged him to "undertake some constructive work in Paleontology in the field and in laboratories" (Numbers, 1992: 89).

The Professor Taber mentioned here was Stephen Taber (1882-1968), who received his A.B. from Stanford University in 1906 and his Ph.D. from the University of Virginia in 1912. Taber, Professor of Geology and Mineralogy at the University of South Carolina from 1912 to 1947 and South Carolina State Geologist from 1914 to 1947, published extensively on a variety of topics, including earthquakes, freezing and thawing of soils, perennially frozen ground, and the Pleistocene geology of the coastal plain (Hollis, 1956: 216-217; Sanders and Anderson, 1999).

Arthur McQuiston Miller (1861-1929) was a geologist at the University of Kentucky, who in his correspondence to Science (Miller, 1922a), cited by Moore, referred to "the geological jugglings of a certain Professor McCready Price" (see Note 38). Later in the same year, Miller (1922b) published an article in Science entitled "The New Catastrophism and Its Defender," in which he presented a brief review of what he called Price's "distinctive ideas" (Miller, 1922b: 701). In commenting upon Price's writings, Miller (1922b: 702) acknowledged that they "possess a certain charm of literary style, and indicate on the part of the author a gift of popular presentation," but lamented that they "had not been devoted to more laudable purpose," and noted that one "must constantly marvel at the character of mind of the man who can so go into the literature of the subject and still continue to hold such preposterous opinions." After reading Miller's uncomplimentary remarks, Price wrote a letter to James McClean Cattell (1860-1944), editor of Science, "threatening 'action for libel' but expressing a willingness to settle for the opportunity to rebut Miller. Cattell offered to correct any errors of fact but declined to print Price's geological views on the grounds that they 'would not be of interest to scientific men'" (Numbers, 1992: 91).

In his memoirs, John Scopes (see Note 50) recalled that Miller was one of his favorite teachers at the University of Kentucky and mentioned that he was called "Monkey" Miller because he taught evolution (Scopes and Presley, 1967: 29).


During the first quarter of the 20th century, Walter L. Brock, in addition to serving as a minister, was associated with a college and a children's home supported by the Baptist Church in Kentucky (Masters, 1953).

George W. Ellis (1861-1934), farmer, tobacconist, and real estate dealer, served for a time as a magistrate and was elected to the Kentucky House of Representatives in November 1921 and served one term (personal communications from: Gerard R. Donovan, 27 January 1998; Pen Bogert, 29 January 1998; Tom Stephens, 29 January 1998; Gayle Alvis, 6 February 1998).

Frank Augustus Miller (1877-1929), attorney, represented Darlington County in the South Carolina Senate from 1919 through 1922 and from 1927 through 1929 (Bailey et al., 1986: 1111-1112).

William Bell Riley (1861-1947), an influential fundamentalist minister, was an outspoken critic of evolution (Numbers, 1992: 45-46).

Professor Dow (1888-?) resigned under pressure despite the fact that he "publicly confessed to having 'made some blunders in expressions' and professed not to believe or teach 'that man came from another species'" (Numbers, 1992: 47). His attacker, J. Frank Norris (1877-1952), pastor of the First Baptist Church in Fort Worth, Texas, found fault with Dow's ideas regarding family life because they supported evolution (Webb, 1994: 71-72). Norris was called by "the Christian Century in 1924... 'probably the most belligerent fundamentalist now abroad in the land.' " (Numbers, 1992: 47).

John Andrew Rice (1882-1930) was born in Colleton County, South Carolina, received the A.B. and A.M. degrees from South Carolina College, and studied at Columbia Theological Seminary and for two years under Old Testament scholars at the University of Chicago. In addition to serving for a short time on the faculty of Southern Methodist University (1920-1921), he served for six years as president of Columbia (South Carolina) College for Women, was pastor of a number of churches in South Carolina, Alabama, Louisiana, Texas, Missouri, and Oklahoma, published four religious books, and edited a Methodist periodical (The Encyclopedia of World Methodism, 1974, Vol. 2, pp. 2011-2012; Who Was Who in America, 1981, Vol. 1 [1897-1942], p. 1027).

Joseph Villiers Denney (1862-1935), Professor of English and Head of the Department of English at Ohio State University from 1904 until his retirement in 1933, author of numerous scholarly works, including textbooks of English, and editor of a number of other studies, was President of the American Association of University Professors from 1921 to 1929 (The National Cyclopaedia of American Biography, 1962, Vol. 44, pp. 285-286).

The material quoted here appeared in a short article clipped from a journal and inserted into the manuscript, but no source was given. The format in the clipping is
similar to that found in two other clippings inserted into the manuscript. Those are from *Science*.

50 During the early 1920s William Jennings Bryan (1860–1925), Democratic and Populist political leader, gifted orator, and three times the unsuccessful candidate (1896, 1900, 1908) for the presidency of the United States, was perhaps the most outspoken opponent of the teaching of evolution in the public schools. In July of 1925 in Dayton, Tennessee, Bryan participated in the prosecution of John Thomas Scopes (1900–1970), a young high school teacher, who had been charged with violating a new law that prohibited teaching the evolution of man in the public schools of Tennessee; Clarence Seward Darrow (1857–1938), one of the most talented trial lawyers in the history of American jurisprudence, led for the defense. Scopes was found guilty and fined $100. The case was appealed to the Supreme Court of Tennessee, which upheld the constitutionality of the law but overruled the lower court on the grounds that Scopes had been fined inappropriately (*Dictionary of American Biography*, 1957–1958, Vol. 2, Part 1, pp. 191–197; 1958, Vol. 11, Part 2, Supplement 2, pp. 141–144; 1988, Supplement 8, pp. 582–584; Scopes and Presley, 1967; Stone, 1971, 480–487, 522–523; Larson, 1985: 58–72; Webb, 1994: 66–93).

What is not always appreciated about the Scopes Trial is that the teaching of evolution was only a minor issue, if, in fact, it were an issue at all. The Trial was really about academic freedom. Lawrence Levine (1968: 331), in his discourse on the last decade of Bryan's life, remarked that

> The Scopes Trial, occupying the center of national attention, offered the friends of academic freedom a rare opportunity to proclaim the essentials of their creed and to point out that while local communities had the unquestionable legal authority to regulate education, there were moral as well as legal limitations to the curb that could be placed upon free speech and thought in the classroom.

Further on, Levine (1968: 354) noted that the Trial, "by dealing Bryan and his fellow fundamentalists some heavy blows and by helping to check the spread of the anti-evolution movement, unquestionably aided the cause of academic freedom."

There is no question that John Scopes understood the significance of the trial, "for he believed that neither politics nor religion should dictate what knowledge people should have" (*Dictionary of American Biography*, 1988, Supplement 8, p. 583). In a speech given in Nashville, Tennessee, in the year of his death, Scopes remarked that "it is the teacher's business to decide what to teach. It is not the business of the federal courts nor of the states" (as quoted in the *Dictionary of American Biography*, 1988, Supplement 8, p. 584).

Although born in Kentucky, Scopes attended high school in Illinois, graduating in 1919 in the town of Salem, the birthplace of William Jennings Bryan, who "spoke there frequently," giving Scopes ample "opportunity to study at leisure the man who would later inspire and assist in [his] prosecution." At Scopes's high-school graduation, Bryan delivered the commencement address and suffered some embarrassment as the result of "a minor slip" during his talk. To Scopes's surprise, Bryan remembered the incident when they met six years later in Dayton (Scopes and Presley, 1967: 15–19, 25–27).

Of passing interest is the fact that John Scopes's wife, Mildred Walker, was from South Carolina. Scopes noted that "after we were married, Mildred told a reporter, 'My aunt thought that Scopes was something with horns on. I never dreamed then that I would meet him and marry him!'" (Scopes and Presley, 1967: 257–258).

Access to new archival material has enabled Edward J. Larson, a professor with a joint appointment in history and law at the University of Georgia, to provide a fresh examination of the Scopes Trial, and, in so doing, to publish an award-winning book (Larson, 1997). Larson received the 1998 Pulitzer Prize in History for his *Summer for the Gods*.


52 Edwin Grant Conklin (1863–1952) became a professor of biology at Princeton University in 1908 and remained there as an independent researcher and lecturer after his retirement in 1933. Conklin made important contributions in studies of invertebrate embryology and cell division and wrote numerous papers on evolution. Beyond the scientific realm, he was curious about the interrelationship of science, philosophy, and society (*Dictionary of Scientific Biography*, 1971, Vol. 3, pp. 389–390; Maimanschein, 1991: 208–229). In his response to Bryan, published in the *New York Times*, Conklin demonstrated a keen sense of humor when he wrote: "Apparently Mr. Bryan demands to see a monkey or an ass transformed into a man, though he must be familiar enough with the reverse process" (Conklin, 1922, Section 7, p. 14).

53 Moore's statement, "All the stages in the development [of a human] conform in the minutest detail to the development of the beasts," was adequate for an educated audience (such as the Cosmos Club) made up mostly, if not entirely, of nonscientists, but is very obviously incorrect. If all human developmental stages conformed in the minutest detail to those of the "beasts," it would be impossible to distinguish human from beast or one species of beast from another. At this point in his essay, Moore seems to be following an old argument which asserted that within a group of organisms, such as the vertebrates, there exists a common pattern of development, resulting in various species of the group resembling each other very closely in their early stages of development and diverging in later stages towards their own specific forms. Such an interpretation "obscures the complex developmental specializations manifest in every species and contravenes . . . [the] generalization that individual
development is truly progressive differentiation” (Coleman, 1977: 50-51).

Moore certainly knew that neither man nor other animals create energy by the oxidation of food (or in any other manner). “Obtains energy” would have been a better phrase to use.

Here Moore overstated his case. See the section entitled “Comments on Moore’s Manuscript” for a different view of the perception of natural selection in the 1920s.

See Note 55.

The array of biologists mentioned here by Moore is strong evidence for his having had a good knowledge of the history of evolutionary biology. Darwin, Huxley, and Wallace are considered elsewhere herein—Darwin and Wallace briefly in Note 8 and Huxley at greater length in Notes 1, 8, and 32. The mention of "Osbourne" was a reference to the paleontologist Henry Fairfield Osborn (see Note 51).

Jean Baptiste Pierre Antoine de Monet, Chevalier de Lamarck (1744-1829), French botanist, zoologist, and paleontologist, was the first person to develop a consistent theory of evolutionary modification. In developing his evolutionary concepts, Lamarck was influenced greatly by his study of fossil and recent mollusks, in which he was able, in some cases, to see almost complete phylectic series. The mechanisms of evolutionary change proposed by Lamarck included the capability of acquiring ever greater complexity and the faculty for responding to special environmental conditions. He considered the strengthening of an organ by use or its weakening by disuse and the inheritance of acquired characteristics to be paramount features of his theory. Lamarck did not propose an hypothesis for the origin of new species, never dealt with the concept of common descent, and ignored the geographic distribution of plants and animals in his evolutionary concept. In contrast with what has been often proclaimed, Lamarck’s model did not include direct environmental induction of new traits nor acts of volition, i.e., the slow willing of useful changes into the biological repertoire of animals (Mayr, 1982: 343-362).

Étienne Geoffroy Saint-Hilaire (1772-1844), French zoologist, made major contributions to the science of comparative anatomy; two principles that he devised for determining homologies are still in use today (Mayr, 1982: 462). Mayr (1982: 362) wrote that “the thesis that Geoffroy in his later years had become an evolutionist is still controversial,” but Bowler (1990: 29) asserted that “in effect, he proposed a theory of evolution by sudden saltations or ‘leaps’ caused when changed conditions disturbed the process of growth and led to the formation of new organic structures.” Geoffroy’s “theory of evolution” was based in large part on his work in teratology. The mechanism he suggested depended on environmental forces acting directly upon the morphology of the developing organism (Appel, 1987: 131-132). “A theory of evolution was almost a necessary corollary of Geoffroy’s general views on God, nature, and natural law, for the alternative was the entirely unacceptable proposition that God had intervened from time to time to create new animals” (Appel, 1987: 184). It is of interest to learn that Geoffroy was a Deist (see Note 8) (Dictionary of Scientific Biography, 1972, Vol. 5, p. 355; Mayr, 1982: 363; Appel, 1987: 7, 24, 138).

Asa Gray (1810-1888), American botanist, friend of Darwin, and devout Christian, was one of a very small number of Darwinians who successfully accommodated belief in a personal God with natural selection, but, in the long run, even he could not reconcile his religious views with the factor of random variation inherent in Darwinian theory (Mayr, 1982: 510; Bowler, 1990: 159).

Louis Pasteur (1822-1895), French chemist, microbiologist, and immunologist, conducted some of the important early work in stereochemistry; demonstrated that microorganisms are the agents of fermentation; provided strong evidence in opposition to the theory of spontaneous generation; studied the causes and developed remedies for a number of infectious diseases, e.g., anthrax, fowl cholera, and rabies; developed measures to control the silkworm blight; received a number of patents or licenses, including those for his methods of making vinegar, manufacturing beer, and preserving wine; and originated the process now known as pasteurization (Dictionary of Scientific Biography, 1974, Vol. 10, pp. 350-353, 372-376; Geison, 1995).

The very careful work of Pasteur and others in discrediting the theory of spontaneous generation created a predicament for evolutionists in search of an explanation for the origin of life (Mayr, 1982: 582). Regardless of the fact that Pasteur campaigned against the idea of spontaneous generation, he, on occasion, speculated about the origin of life and even made efforts to produce or modify it in the laboratory. Although Pasteur was clearly skeptical about Darwinian theory per se, it is difficult to pin down his general attitude towards organic evolution. In a lecture given on 22 December 1855, Pasteur seemed to adopt a concept of life that was at the same time materialistic and spiritualistic (Dictionary of Scientific Biography, 1974, Vol. 10, pp. 355, 382; Farley and Geison, 1974: 172-179, 188-198; Geison, 1995: 43, 138-142). Pasteur’s ambivalence and the fact that Darwin was never supported by any of the important French biologists of the mid-19th century are more understandable when one becomes aware of the religious and political climates of France during the years immediately following the publication of the Origin of Species. At that time it was impossible for Darwinism to become established because French biology included not only science but also religion and political philosophy, and all were hostile to new ideas (Farley, 1974: 279, 287-290, 300).

The German August Friedrich Leopold Weismann (1834-1914) has been called by Ernst Mayr (1982: 698) “one of the great biologists of all time.” He worked on a great diversity of problems, but genetics and evolution were his major interests. Modern genetics is supported by the foundation built by Weismann. His theory of evolution rejected all belief in the inheritance of acquired characteristics and has been termed neo-Darwinism. He is also well remembered for his theory of the “continuity of the germ plasm” (Mayr, 1982: 698, 700, 706).

The German zoologist Ernst Heinrich Philipp August Haeckel (1834-1919) became an enthusiastic evolutionist after reading the Origin of Species (Dictionary of Scientific Biography, 1972, Vol. 6, pp. 6-9; Mayr, 1982: 555; Bowler, 1990: 144), but he is said to have “had little understanding of natural selection” and has been called a pseudo-Darwinian (Bowler,
Edward Drinker Cope (1840–1897), American paleontologist and zoologist, became an important neo-Lamarckian in the late 1860s (Bowler, 1990: 175). Neo-Lamarckism shared with Lamarck's theory "improvement of adaptation (neglecting or disregarding altogether the origin of diversity)" and inheritance of acquired characteristics (Mayr, 1982: 526). (See Note 51.) Although reared as a Quaker and fervently religious for a time, as a young man, Cope resigned from the Society of Friends after his father's death and eventually became a Unitarian (see Note 8) (Osborn, 1931; Lanham, 1973: 68; Sho, 1974: 14–15; Davidson, 1997).

George John Romanes (1848–1894) was a Canadian-born British physiologist and comparative psychologist, who worked on invertebrate nervous systems, became a close associate of Darwin, and developed a strong interest in mental evolution, writing on that topic and other aspects of evolution (Dictionary of Scientific Biography, 1975, Vol. 11, pp. 516–530; Bowler, 1990: 193).

As indicated in Moore's remarks, the horses, Family Equidae, do have an extensive and well-studied fossil record, but the earliest recognized member of the family, *Hyracotherium (=Eohippus)*, "known from the base of the Eocene in both North America and Europe," had four toes on each front foot and three on each rear one (Carroll, 1988: 533).

Josh Billings was the pen name of Henry Wheeler Shaw (1818–1885), an American humorist, who enjoyed wide popularity after the Civil War as a result of his comic writings and oral presentations (Dictionary of American Biography, 1964, Vol. 9, Part 1, pp. 39–40).

*Archeopteryx* is in reality late Jurassic in age and is known from a small number of fossils obtained from lithographic limestone in the Solnhofen region of west central Bavaria, southern Germany (Carroll, 1988: 338, 580).


In 1886, de Vries found growing in a large population of *Oenothera lamarkiana* two plants that he considered to be different enough from the others present to warrant recognition as a distinct species and eventually discovered more than 20 individuals originating from *Oenothera lamarkiana* that he regarded as new species (Mayr, 1982: 742). The production of these "new species" were the result of a variety of genetic alterations, especially chromosomal aberrations (Dobzhansky et al., 1977: 59).

Tschermak apparently lacked the understanding of Mendism displayed by de Vries and Correns (Stenni and Stern, 1978: 237–240), and perhaps, as suggested by Mayr (1982: 750), there is "little justification" for considering him a rediscoverer.

Thomas Hunt Morgan (1866–1945) was an American geneticist, embryologist, cytologist, and evolutionary biologist, who, along with his coworkers at Columbia University, made some of the most significant contributions to the elucidation of the roles of genes and chromosomes in inheritance. Morgan received the Nobel Prize in medicine or physiology for 1933 for his signal efforts in establishing the chromosome theory of heredity. He was, in fact, the first researcher not working in a strictly physiological area to be awarded the Nobel Prize in that category (Dictionary of Scientific Biography, 1974, Vol. 9, pp. 515–526; Allen, 1978; Mayr, 1982: 752–760, 764–775; Maienschein, 1991: 231–260).

Moore's statement that "Morgan...has seen the same thing with the...fruit fly" is not correct in view of current knowledge. Dobzhansky et al. (1977: 188) remarked that the "mutations observed by Morgan were not new species but variant forms of the ancestral one."

The material in brackets was added by Moore.


William Patten (1861–1932), zoologist and paleontologist, and for 36 years a professor of zoology at Dartmouth College, was especially interested in evolution, publishing on that subject and a number of others, including invertebrate anatomy and embryology, vision, and Devonian fishes. He was a strong proponent of the "Arachnid Theory of the Origin of Vertebrates" and spent more than 30 years in search of fossils of the primitive jawless heavily armored fishes (or fishlike vertebrates) known as ostracoderms (The National Cyclopedia of American Biography, 1935, Vol. 24, pp. 121–122; Dictionary of American Biography, 1962, Vol. 7, Part 2, pp. 300–301).

Patten's address was published in *Science* (Patten, 1920).

On 8 August 1997 the resolution requiring a disclaimer in Tangipahoa Parish, Louisiana, was thrown out by the United States District Court for Eastern Louisiana, the court finding that the disclaimer violated both the constitution of Louisiana and the First and Fourteenth Amendments of the United States Constitution (Matsumura, 1997: 5–6). In a letter dated November 1997, Eugenie C. Scott, Executive Director of the National Center for Science Education (Berkeley, California), informed the members of that organization that in 1997 two school districts in Virginia had considered requiring textbooks to carry disclaimers for evolution and that one of those districts has a pending lawsuit. "The really bad news," she noted, "... is that even after the Tangipahoa decision was announced, a town in Pennsylvania decided to institute a disclaimer."
REPEATABILITY: The same phenomenon is sought again, preferably by independent investigation, and the interpretation given to it is confirmed or discarded by means of novel analysis and experimentation.

ECONOMY: Scientists attempt to abstract the information into a form that is both simplest and aesthetically most pleasing—the combination called elegance—while yielding the largest amount of information with the least amount of effort.

MENSURATION: If something can be properly measured, using universally accepted scales, generalizations about it are rendered unambiguous.

HEURISTICS: The best science stimulates further discovery, often in unpredictable new directions; and the new knowledge provides an additional test of the original principles that led to its discovery.

CONSILIENCE: The explanations of different phenomena most likely to survive are those that can be connected and proved consistent with one another.

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Systematics and Biogeography of the \textit{Notropis rubellus} Species Group (Teleostei: Cyprinidae)

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ABSTRACT: Wood, Robert M., Richard L. Mayden, Ronald H. Matson, Bernard R. Kuhajda, and Steven R. Layman. 2002. Systematics and biogeography of the \textit{Notropis rubellus} species group (Teleostei: Cyprinidae). Bulletin Alabama Museum of Natural History, Number 22:37-80, 5 tables, 7 figures, 1 appendix. The rosyface shiner, \textit{Notropis rubellus} has long been recognized as a single, widespread species exhibiting geographic variation in morphological characters. The \textit{Notropis rubellus} species group is distributed widely throughout highland and glaciated regions of eastern North America. The systematics of this species group is investigated herein through both population genetic and phylogenetic analyses of 37 presumptive gene loci in 33 populations from throughout its range. Analysis of these data suggest the current taxonomy employed for \textit{N. rubellus} does not reflect existing patterns of genetic divergence, cladogenesis and phylogenetic affinity within the species group, or between members of this group and other closely related species. Based on these data we recommend taxonomic changes for members of the \textit{N. rubellus} species group to more accurately reflect historical patterns of divergence and cladogenesis among these fishes. In addition to an undescribed species in the upper New River identified in this study and the recently described \textit{N. sulikui}, phylogenetic and population genetic analysis of the allozyme data support the recognition of three additional allopatrically distributed species currently recognized under \textit{N. rubellus}. These include \textit{N. rubellus} (rosyface shiner), \textit{N. micropteryx} (highland shiner), and \textit{N. percophthalmus} (carmine shiner). \textit{Notropis rubellus} is distributed in the Great Lakes basins; the Ohio River basin above the Green River, excluding the upper New River; and some Atlantic Slope drainages. \textit{Notropis micropteryx} is restricted to the Green, Cumberland, and Tennessee river systems. \textit{Notropis percophthalmus} is found in rivers of the upper Mississippi River basin, the Wabash River system, rivers of the Ozark Highlands, and the upper Ouachita River system. The existence of various distinct forms within \textit{N. percophthalmus} supported by morphological and allozyme characters and phylogenetic analyses of allozyme data may eventually warrant taxonomic recognition. Phylogenetic relationships resolved among these taxa indicate that the undescribed species from the New River forms the sister species to all remaining members of the group. Relationships among remaining taxa resolve \textit{N. micropteryx} as the sister taxon to \textit{N. rubellus} plus a clade of \textit{N. percophthalmus} and \textit{N. sulikui}. The general correspondence between phylogenetic relationships among these species and the Teays-Mississippi and Laurentian waterways provide compelling evidence for a pre-Pleistocene origin of the speciation events leading to diversification within these taxa.

Introduction

The rosyface shiner, \textit{Notropis rubellus} (Agassiz, 1850), is one of the most geographically widespread members of \textit{Notropis}. The distribution of this species has traditionally extended from the north Atlantic Slope in Virginia to the St. Lawrence seaway, westward across the Great Lakes drainages and upper Ohio, Mississippi, and Missouri rivers to the Red River in Manitoba, and south to the Red River in Oklahoma and the Tennessee River in northern Alabama. Throughout its range, populations of the \textit{N. rubellus} species group generally are confined to clear,
high-gradient creeks and rivers of upland areas. This species group is fragmented into many smaller geographic components, separated by less favorable habitats associated with larger rivers and their floodplains and landscapes formerly impacted by glaciation.

The broad distribution of this species has precluded any thorough systematic analyses. As of 1978 Gilbert commented that the systematics of the group had not been adequately studied (Gilbert, 1978:61). Not until recently has this species been the subject of any systematic studies (see also Humphries and Cashner, 1994 for review). Efforts at revealing natural patterns of variation have focused on regional diversity utilizing morphological characters. This also includes the most recent analysis of some populations within *N. rubellus* by Humphries and Cashner (1994) wherein *N. suttkusi* was described from the Red River drainage in the Ouachita Highlands. While various names have been applied to members of this species group their application to geographic components within *N. rubellus* has not been accompanied by a thorough and inclusive analysis of variation throughout the range of the species.

Although the geographic distribution and taxonomic history of the *N. rubellus* species group has complicated our understanding of its evolutionary history and diversity, this group offers unique opportunities to gain insight into speciation and biogeography within the North American ichthyofauna. The *N. rubellus* species group inhabits waterways and geographic areas that together comprise the former Central Highland region, a pre-Pleistocene, contiguously distributed composite of provinces once characterized by clear, cool high-gradient streams. The biota inhabiting this region was extensively impacted by glacial processes that resulted in dramatic changes in river systems and their species communities. These processes have been invoked by some as the fundamental causal mechanism precipitating speciation in the Pleistocene landscape (Burr and Page, 1986; Starnes and Etnier, 1986; McKeown et al., 1984). Others have argued that much of the speciation within the Central Highlands fauna predates the Pleistocene and that glacial processes were primarily responsible for the extinction of some species extant at that time (Mayden, 1987a, b; 1988a, b). Largely missing from these studies have been clades containing taxa with wide-ranging distributions and populations found in both glaciated and unglaciated drainages; both of these are characteristics of the *N. rubellus* species group. Evaluation of clades possessing these characteristics not only enhances our resolution of the biogeographic history of this region, but also extends special opportunities to compare anagenetic and cladogenetic histories of populations and/or species that existed in drainages variably impacted by glacial processes.

This study examines genotypic variation within the *N. rubellus* species group from throughout its range. Patterns of allozyme variation, interpreted in concert with variation in close outgroup species, is employed to discern the natural diversity within the group and determine the phylogenetic relationships of its component species. These patterns are interpreted in light of the geological histories of river systems currently and formerly inhabited by these shiners to better understand species and genetic diversity within the group and the biogeographic history of the Central Highlands ichthyofauna as a whole.

**Methods**

Methods for allozyme electrophoresis and data analysis generally followed those described by Wood and Mayden (1992) and Mayden and Matson (1992). Buffer systems were provided in Mayden and Matson (1992). For the data analysis BIOSYS-1 (Swofford and Selander, 1981), FREQPARS (Swofford and Berlocher, 1987), and PAUP (version 3.1.1, Swofford, 1992) were employed in the population genetic and phylogenetic analyses. Genetic distances included Rogers (1972), Modified Rogers (Wright, 1978), Prevosti (Wright, 1978), and Cavalli-Sforza and Edwards (CS&E) (1967) arc and chord. Topologies generated from distance Wagner and PAUP analyses and additional, manually generated topologies were evaluated for overall FREQPARS length to determine most parsimonious topologies.

For the discrete character analysis employed in PAUP (Swofford, 1992) the locus was considered the character and combinations of alleles within a taxon represented character states. Character states were coded using two methods following Buth (1984) and Mayden and Matson (1992). Phylogenies were generated from both methods of coding using Fitch parsimony (1971; unordered). Generalized parsimony (Swofford and Olsen, 1990) was used to generate phylogenies with the qualitative coding methods and was accomplished through the use of stepmatrices constructed for each locus (Mabee and Humphries, 1993). Stepmatrices were calculated using a customized C program (Mayden, Sankar, and Wood, unpubl. data). This method of parsimony may be more realistic relative to the evolution of alleles within a locus compared to Fitch parsimony where, in the latter, changes between different allelic combinations (e.g., allele A present at a locus = Code 1, AB = 2, BC = 3, CD = 4) all have equal lengths. Under this method the number of steps between combinations of alleles present in a species at a locus is the number of the changes required to gain and/or lose alleles between allelic combinations. To go from a combination of A to AB is one step, the gain or loss of B; to go from BC to CD is two steps, the gain/loss of both alleles B and D. Both the Fitch and Generalized parsimony methods were derived using all alleles and a reduced data base where "rare" alleles (frequency < 0.10) were eliminated. The consistency index (CI) and retention index (RI) is provided in trees derived using Fitch parsimony.
These indices are not provided for trees derived using generalized parsimony because it is impossible to calculate minimum lengths required for stepmatrix characters (D. L. Swofford, pers. comm.).

The expansive range of the N. rubellus species group precluded the use of large numbers of specimens from each sample. Although Gorman and Renzi (1979) concluded that sample sizes as small as a single individual were sufficient for the production of allozyme frequency-based phylogenies, Archie et al. (1989) indentified potential problems with sample sizes this small. To avoid these potential problems sample sizes in this study ranged from 10 to 23 specimens from 33 populations throughout the range of the N. rubellus species group.

Outgroup taxa in this study included N. atherinoides, N. stilbius, and N. photogenis. Based on findings by Mayden and Matson (1988) and Dowling (1991) that N. rubellus, N. stilbius, and N. atherinoides formed a clade sister to N. photogenis we used the latter species as the basal-most outgroup taxon to root trees.

Throughout the text the following river and geographic notations are used. The upper Ohio River refers to tributaries of the Ohio River above the mouth of the Green River, exclusive of the New River. The New River refers to both the New and Kanawha rivers above Kanawha Falls. The Tennessee River includes all tributaries of this river as well as the Duck River. Lake Michigan refers to the sample from St. Joseph River. The Wabash River is divided into a lower, middle, and upper Wabash; upper Wabash includes Tippecanoe River, middle Wabash includes Vermillion River, and lower Wabash includes East Fork White River. Rivers of the Ozarks refer to both the northern drainages (Meramec, Gasconade, Osage, and Kansas) and southern drainages (Current, White, and Arkansas). Missouri River drainage includes the Gasconade, Osage, and Kansas rivers. Ouachita Highland rivers include the Ouachita, Kiamichi, and Blue rivers. Rivers of the Interior Highlands include all Ozarkian and Ouachita highland rivers. The Western Highlands includes the Interior Highlands and tributaries of the upper Mississippi River as far north as the unglaciated region in Illinois, Wisconsin, and Iowa. Finally, the Notropis rubellus species group refers to all diversity currently referred to N. rubellus and N. suttkusi. Institutional abbreviations follow Leviton et al. (1985) and Leviton and Gibbs (1988).

Results
Taxonomic Changes.— Given the observed significant patterns of allozyme variation, patterns of genetic subdivision, and the phylogenetic relationships among diagnosable clades within the N. rubellus species group presented below, the current taxonomy employed for these fishes does not accurately reflect detectable historical patterns of cladogenesis and genealogical affinities. The following taxonomic changes are recommended for the N. rubellus group to better reflect divergence patterns within this group as independent lineages viewed as species sensu the Evolutionary Species Concept (Mayden and Wood, 1995; Mayden 1997; Wiley and Mayden, 2000a, b, c) and diagnosable by the Phylogenetic Species Concept (sensu Mayden, 1997). In addition to the undescribed species in the upper New River identified in this study and the recently described N. suttkusi (Humphries and Cashner, 1994), at least three species are recognized as currently masquerading under the single name Notropis rubellus: N. rubellus, N. micropteryx, and N. percobromus. Additional variation and species diversity likely exists in the Interior Highands but deserves additional study.

Notropis rubellus (Agassiz)
rosyface shiner

Figure 1A.


Leuciscus copii Günther 1868:255-256 [original description; type locality: St. Joseph River and Dowagiac Creek (trib. to St. Joseph River), Berrien Co., Michigan; synotypes: ANSP 2577 (42.0), MCZ 4688 (2, 50.6-55.2), MNHN 4688 (2, 42.6-44.4)].—Gilbert 1978, 1998 (type catalogues; discussion of types, localities, emendation of name, and Alburnus rubellus as junior synonym).

Alburnus jacobus Günther 1867:387-388. [original description; type locality: St. Joseph River and Dowagiac Creek (trib. to St. Joseph River), Berrien Co., Michigan. ANSP 2577 (42.0), MCZ 4688 (2, 50.6-55.2), MNHN 4688 (2, 42.6-44.4). based on same type materials as Leuciscus copii].—Gilbert 1978, 1998 (type catalogues; discussion of previous misidentifications, types, synonyms, and Günther’s designation as junior synonym of Leuciscus copii).

Types: Syntypic series of N. rubellus included 14 specimens later determined to be a mixed collection of N. atherinoides (9 spms) and N. rubellus (5 spms). Those of N. atherinoides were collected from “the Pic” and specimens of N. rubellus were collected from Lake Superior, at Sault
Figure 1. Members of the *Notropis rubellus* species complex. A) *Notropis rubellus* (Clear fork, Whitley Co., Kentucky). B) *Notropis micropteryx* (Powell River, Claiborne Co., Tennessee). C) *Notropis percobromus* (Big Piney River, Texas Co., Missouri). (Photographs by David J. Eisenhour and used with permission.)
Figure 2. Hypothesized geographic distributions of species in the Notropis rubellus species complex based on geographic variation of allozyme products.

Ste. Marie, either Michigan or Ontario. Paratopotypes include MCZ 91786 (formerly MCZ 1749A) (4) and UMMZ 87100 (formerly MCZ 91786, formerly MCZ 1749A) (1).

Distribution: Drainages of the Great Lakes, waterways of the upper Ohio River (above the mouth of the Green River, exclusive of the New River above Kanawha Falls), northern Atlantic Slope, and Cumberland River above the Cumberland Falls (Fig. 2).

Comments: Hubbs and Brown (1929:35) and Gilbert (1978) discussed the mixed syntypic series for the rosyface shiner. The former authors designated the type locality as Sault Ste. Marie, based primarily on the quote from Agassiz’s description “The species is very common at the Sault of St. Mary; specimens were also obtained at the Pic.” They also identified what they thought to be Agassiz’s holotype as a tintagged and morphologically aberrant specimen that was illustrated in Agassiz’s description. While N. rubellus had long been considered conspecific with N. atherinoides up to that time, even by Hubbs and Greene (1928:381), Hubbs and Brown (1929) were confident that N. rubellus represented a distinct species and one conspecific with N. rubriprons (Cope), a name currently in use at that time.

Notropis micropteryx (Cope)

highland shiner

Figure 1B.

Alburnellus micropteryx Cope, 1868:233 [original description; type locality: Holston River, Virginia; lectotype:

Types. This species was described from two specimens collected from the Holston River, Virginia. Paralectotype: ANSP 2843 (54.9). Lectotype designated by Fowler (1910: pl. 21, fig. 64) by illustration of “type.”

Distribution: Restricted to the tributaries of the Green, Cumberland (below Cumberland Falls), and Tennessee rivers in Kentucky, Tennessee, Alabama, Virginia, and North Carolina (Fig. 2).

Comments: This study reveals limited variation for this species within and between the Cumberland and Tennessee river populations, based on allelic variation and F statistics. However, considerable variation does exist between N. micropteryx from the Green River relative to those populations in the Cumberland and Tennessee rivers. Further investigation of morphological and/or molecular data may be useful in further resolving relationships among populations within this species.

**Notropis percobromus (Cope)**

carmine shiner

Figure 1C.

*Alburnellus percobromus* Cope 1871:440 [original description; type locality: St. Joseph, Missouri; lectotype: ANSP 2993 (39.5), Dr. William Stimpson, no date].

Types. Syntypic series consisted of 14 specimens from near “St. Joseph, Missouri.” Paralectotypes: ANSP 2994-3009 (13), Dr. William Stimpson, no date. Lectotype designated by Fowler (1910: pl. 21, fig. 60) by illustration of “type.”

Distribution: Inhabits rivers and streams draining into the Wabash River, northward and westward in the upper Mississippi and middle Missouri rivers in Illinois, Wisconsin, Minnesota, Iowa, North and South Dakota, Kansas, and Missouri, southwestward in the Missouri and Arkansas rivers in Kansas, Oklahoma, and Arkansas, and the Ouachita River in Arkansas. When formerly recognized as a full species, earlier researchers recorded this species as ranging “from the Red and Arkansas river systems in the Great Plains of Oklahoma and Kansas to the Mississippi River in Tennessee, northward through Nebraska, Missouri, and Iowa to the Missouri River system in the Dakotas and to the Mississippi River between Minnesota and Wisconsin” (Bailey and Allum, 1962). Unfortunately, until 1978, *N. percobromus* was largely confused with *N. atherinoides* (Gilbert, 1978, 1998; Humphries and Cashner, 1994).

Comments: Gilbert (1978:68-69) and Humphries and Cashner (1994) discussed some of the troubled taxonomic history that *N. percobromus* has survived with *N. rubellus* and *N. atherinoides*. Long considered a synonym of *N. rubriformis (N. rubellus)* after Jordan (1885), Hubbs and Ortenburger (1929) considered it to be a valid southwestern *Notropis*, distinct from *N. rubellus* and *N. rubriformis*. Hubbs (1945), Hubbs and Bonham (1951), and Hubbs and Lagler (1958:81) later reversed this opinion. Bailey (1951:192; 1956:382) and Bailey and Allum (1962) were skeptical as to the distinctiveness of *N. percobromus* from *N. atherinoides* and attributed the multiple, syntopic series of both species collected by G. A. Moore and C. L. Hubbs, and identified by the latter, as having resulted from environmentally induced variation maintained over several years. Unfortunately, types of *N. percobromus* were not examined by any of these researchers to resolve this confusion. Gilbert (1978) identified the types as a *N. rubellus* form, distinct from *N. atherinoides*. Gilbert (1978) thought that *N. percobromus* may represent a valid form, but tentatively regarded it a junior synonym of *N. rubellus* until further study.

Populations of *Notropis percobromus* are paraphyletic with respect to *N. suttkusi*. In all phylogenies the Ouachita River population of *N. percobromus*. In all phylogenies the Ouachita River population of *N. percobromus* was found to be more closely related to *N. suttkusi* than to any other conspecific samples. Furthermore, in several phylogenies, populations from rivers of the southern Ozarks were more closely related to the Ouachita River populations and *N. suttkusi* than they were to northern populations of *N. percobromus*. Our current recognition of all these populations under *N. percobromus* is a matter of convenience. Interestingly, early morphological studies by C. L. Hubbs (Hubbs and Ortenburger, 1929) led him to identify more than one nominal, yet undescribed form within rivers of the Ozark uplands. Among other forms identified, Black (1940), Aldrich (1946), and Humphries and Cashner (1994) used Hubbs’ manuscript names *N. r. rubricorpus* and *N. r. retrivelis* as *nomen nudum* for forms known to occur in the Arkansas River in Missouri, Kansas, Oklahoma, and Arkansas, and the White, St. Francis, Whitewater, and Castor rivers in Missouri and Arkansas, respectively. Patterns of allozyme variation, phylogenetic relationships of populations, and extent of **F** _st_ variation among samples of *N. percobromus*, especially those from the Ozark Highlands, are consistent with Hubbs’ earlier hypotheses of diversification. Future morphological and/or molecular studies will likely indicate that populations from some Interior Highland rivers, together with those from the eastern Ouachita Highlands, may warrant species recognition. Populations in the Wabash River system display patterns of genetic variability worthy of further, more thorough investigation.
Notropis suttkusi
Humphries and Cashner
rocky shiner

Notropis suttkusi Humphries and Cashner 1994:82-90
[original description; type locality: Little River at Cow Crossing, 16 km E of Idabel, T7S, R26E, Sec. 15NE, NE1/4, McCurtain Co., Oklahoma, 16 July 1990, F. P. Gelwick, W. J. Matthews, C. Vaughan, and M. Winston].

Types. A total of 382 type specimens were designated from the Little, Blue, and Kiamichi rivers in Oklahoma and Arkansas. Holotype: CU 72190 (44.4). Paratypes: Specimens were deposited at CU, NLU, OSUS, OU, SIUC, TU, UF, UMMZ, USNM, UT, UAIC, UNO.

Distribution: Humphries and Cashner (1994) restricted this species to the Blue, Boggy, Kiamichi, and Little rivers of the Red River Drainage in the western Ouachita Highlands (Fig. 2).

Comments: Humphries and Cashner (1994) were unable to confidently classify Ouachita River samples from the N. rubellus species group. Some specimens from the Ouachita River were morphologically similar to N. suttkusi for some characters, but were more like N. rubellus for others. Citing preliminary allozyme variation from this study, these authors suggested that perhaps the samples examined in their morphometric and meristic analyses were of hybrid origin and thus shared characters of both species. They further suggested that either one or perhaps both species may have formerly existed in the Ouachita River, and have subsequently undergone introgression or hybridization. Alternatively, they suggested that a more likely explanation is that one species may have been native, but rare to the Ouachita River and a recent bait-bucket introduction of the other species resulted in a breakdown of their genetic boundaries.

Allozyme variation and population genetics pertinent to these hypotheses are presented below. In the present study, Notropis percobromus from the Ouachita River of the eastern Ouachita Highlands is a diagnosable and divergent form and was consistently recognized as more closely related to N. suttkusi than to any other populations of N. percobromus.

Allozyme Variation
The products of 37 loci were resolved for 33 samples of the ingroup Notropis rubellus species group, and three outgroup species, N. atherinoides, N. stilbius, and N. photogenis. Four loci (Ak-A, mlcdh, Ldh-B, and Sod) were monoallelic for all ingroup and outgroup samples. For the remaining 33 loci geographic variation in the ingroup and phylogenetic variation for the ingroup and outgroups is provided in Appendix 1. Within the ingroup samples the mean number of alleles per locus, proportion of polymorphic loci, and observed and expected mean heterozygosity are provided in Table 1.

Substantial allelic divergence occurred at 16 loci for representative populations or groups of populations across the range of the ingroup. Variation at these loci is discussed under Phylogenetically Informative Loci within the N. rubellus Species Group. Another 17 loci exhibited limited variation within the ingroup, with only rare, primitive and/or derived alleles (relative to outgroups) occurring sporadically over its entire range (Appendix 1; mAat-A, sAat-A, mAcon, sAp-A, Ck-A, Ck-B, Est-I, G3pdh-A, G6pdh-A, Gpi-A, slddh-B, sMdhp-A, dMan, Pk-A, Pnp-A, Tpi-A, Tpi-B). Eight of these loci also possess variation that is informative with respect to the phylogenetic relationships of the N. rubellus species group relative to outgroup taxa. These include sAat-A, mAcon, sAp-A, Ck-A, Est-I, G6pdh-A, Pk-A, and Pnp-A and are discussed below under Additional Phylogenetically Informative Loci.

Phylogenetically Informative Loci within the N. rubellus Species Group

Acp-A.—Notropis stiibius, N. atherinoides, and most populations of N. rubellus species group possessed the derived allele Acp-A(C) relative to the condition possessed by N. photogenis. A retained low-frequency expression of the plesiomorphic allele Acp-A(A) occurred in some N. micropteryx from the Cumberland and Tennessee rivers and N. percobromus from the upper Mississippi River. Acp-A(D) was unique to some populations of N. percobromus from the Interior Highlands and N. suttkusi. Acp-A(B) occurred in low frequency in the Holston, Kentucky, and Big Sandy rivers, and was in high frequency in some Missouri River samples, where fixed in N. percobromus from the Kansas River Drainage.

Ald-A.—The distinct outgroup N. photogenis possessed Ald-A (A), while Ald-A (D) was found only in N. atherinoides. Most populations of the N. rubellus species group possessed a combination of alleles Ald-A (B, C), the latter allele shared with only one outgroup, N. stilbius. The derived allele Ald-A (B) was lost in Notropis suttkusi and N. percobromus from the Ouachita River and the southern Ozarks, some populations of N. micropteryx, and N. rubellus from the Susquehanna River.

Cbp-1.—Members of the N. rubellus species group were fixed for either of two alleles at this locus. Cbp-1 (A) was unique to N. micropteryx (exclusive of Green R.), as well as the most distant outgroup, N. photogenis. All other ingroup samples possessed Cbp-1 (B), an allele considered derived relative to N. photogenis, but shared, primitive within the N.
Table 1. Genetic variability at 33 loci in all populations within the *Notropis rubellus* species group (standard errors in parentheses).

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<th>Mean no. of alleles per Locus</th>
<th>Percentage of loci polymorphic</th>
<th>Mean heterozygosity</th>
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A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.95.

*Unbiased estimate (see Nei, 1978)
rubellus group given that the two nearest outgroups (N. stiltius, N. atherinoides) shared this mobility.

Cbp-2.—Ingroup and outgroup samples expressed one of two different allelic products at this locus. All outgroups, *N. suttkusi*, and *N. percobromus* from the upper Mississippi River and Interior Highland rivers possessed Cbp-2 (B). All other samples were fixed for the alternative allele, Cbp-2 (A).

Est-2.—Most ingroup and outgroup samples were highly polymorphic at this locus. Exceptions included the fixation of Est-2 (D) in *N. suttkusi*, *N. percobromus* from the Ouachita River, and *N. rubellus* from the Atlantic Slope; the fixation of Est-2 (B) in *N. percobromus* from the Missouri River and the geographically adjacent Meramec River; and the fixation of Est-2 (C) in *N. sp.* (New R.). *Notropis photogenis* was fixed for Est-2 (C), while *N. stiltius* and *N. atherinoides* both possessed Est-2 (D, E, F). Among the variable ingroup populations, Est-2 (E) was widespread throughout the group except in *N. rubellus* from the Atlantic Slope, *N. suttkusi*, and *N. percobromus* from the lower Wabash River, upper Mississippi River, and all Interior Highland rivers. Est-2 (D) was essentially restricted to *N. rubellus*, being absent in *N. micropteryx* and *N. percobromus* from all Ozark Highland rivers and the upper Mississippi River. The rare and derived Est-2 (B) occurred sporadically in *N. micropteryx*, was consistently present in low frequency in samples of *N. percobromus* from the upper Mississippi, Wabash, and all Ozarkian rivers and *N. rubellus* from the Great Lakes, but was absent from other *N. rubellus* from the Ohio River tributaries and the Atlantic Slope.

Gpi-B.—The plesiomorphic Gpi-B (C), present in outgroups was widespread in the *N. rubellus* species group. The derived Gpi-B (B) occurred frequently in *N. percobromus* from the Missouri River and rarely in two Tennessee River populations of *N. micropteryx*. *Notropis* sp. (New R.) possessed a rare, but unique Gpi-B (E).

sIcdh-A.—Outgroup species, *N. sp.* (New R.), *N. rubellus* from the upper Ohio, Atlantic Slope, Great Lakes, and *N. micropteryx* were fixed for sIcdh-A (D). The derived alleles sIcdh-A (B, C) occurred in high frequencies and were unique to *N. suttkusi* and *N. percobromus* from the Illinois, Wabash, and upper Mississippi rivers and rivers of the Interior Highlands. The plesiomorphic allele sIcdh-A (D) occurred in relatively high frequency in the lower Wabash and Ouachita river samples of *N. percobromus*. The apomorphic allele sIcdh-A (A) occurred rarely only in the Cumberland River, but commonly in the Ouachita River samples.

sIcdh-B.—*Notropis stiltius*, *N. atherinoides*, and most populations of the *N. rubellus* group possessed only sIcdh-B (A), while *N. photogenis* was fixed for sIcdh-B (B). The rare, derived sIcdh-B (C) occurred only in the Cumberland and Tennessee river samples of *N. micropteryx*.

Ldh-A.—*Notropis photogenis* was fixed for Ldh-A (A). *Notropis stiltius*, *N. atherinoides*, and all ingroup members outside of the Interior Highlands and upper Mississippi rivers shared a fixed, plesiomorphic Ldh-A (C). The derived Ldh-A (D) occurred in *N. percobromus* from the upper Mississippi River tributaries and all the Interior Highlands samples, exclusive of the Ouachita River. The latter population shared the plesiomorphic Ldh-A (C) with the geographically proximate *N. suttkusi*.

mMdah-B.—Relative to outgroup taxa, two derived alleles occurred at this locus. The allele sMdah-A (C) was restricted to samples from the Interior Highlands, upper Mississippi River, and the lower Wabash River. This allele occurred in high frequency in all samples of *N. suttkusi* and *N. percobromus* except in the Wabash River where it was rare. The alternative allele, sMdah-A (A) occurred sporadically and in low frequencies across the range of the *N. rubellus* group. The most frequently observed allele in samples other than listed above was the same product observed in *N. stiltius* and *N. atherinoides*, *N. photogenis* possessed a fixed, unique sMdah-A (D).

sMdh-A.—With the exception of a single putative hybrid individual of *N. photogenis* from the lower Wabash River, all outgroups possessed a single allele at this locus, sMdh-B (C). Within the *N. rubellus* species group all samples except *N. sp.* (New R.) and those from *N. micropteryx* from the Stones River and *N. rubellus* from Lake Michigan shared a derived allele sMdh-B (A). These latter samples were fixed for the plesiomorphic allele. As with the electromorph at the Ck-A locus, the occurrence of sMdh-B (A) in the same specimen of *N. photogenis* from E. Fk. White River is speculated to have resulted from hybridization with sympatric *N. rubellus* in the lower Wabash River.

mMdahp-A.—Most samples possessed one or more plesiomorphic alleles mMdahp-A (A, C, D, E). The derived allele mMdahp-A (B), not found in any outgroups, commonly occurred in *N. micropteryx*, *N. rubellus*, and *N.
percobromus from the Illinois and middle and upper Wabash rivers. Notropis suttkusi and N. percobromus from the Interior Highlands, upper Mississippi River, and lower Wabash River lacked mMdhp-A (B), and shared plesiomorphic allelic compositions. Notropis sp. (New R.) was fixed for the plesiomorphic mMdhp-A (E).

Mpi-A.—The plesiomorphic allele Mpi-A (C) was fixed in all outgroup samples and N. sp. (New R.), as well as in many populations of N. percobromus and one population of N. micropteryx. Derived alleles Mpi-A (A, B, D) occurred sporadically within all other populations.

Pep-A.—All samples of the N. rubellus species group and two outgroup species commonly possessed the derived allele Pep-A (B) relative to Pep-A (A) of N. photogenis. The plesiomorphic allele was rare in N. rubellus from Lake Michigan, N. percobromus from the upper Mississippi River, and N. suttkusi from the Kiamichi River.

Pgk-A.—Most members of the N. rubellus species group shared the common allele Pgk-A (C). Notropis photogenis possessed only allele Pgk-A (A). The plesiomorphic allele Pgk-A (D) was fixed in N. suttkusi, and occurred sporadically in populations of the N. rubellus group.

Pgm-A.—Most members of the N. rubellus group were polyallelic at this locus for the plesiomorphic Pgm-A (B) and the derived Pgm-A (A). Exceptions included the fixation of the Pgm-A (A) product in N. sp. (New R.) and in scattered populations in N. rubellus and N. micropteryx; and the absence of the derived product Pgm-A (A) in N. suttkusi and all N. percobromus from the Interior Highlands (excluding rare occurrence in the Osage River). Notropis suttkusi from the Kiamichi River were fixed for the derived Pgm-A (D), an allele unique among samples from the Interior Highland rivers but a product occurring in low frequency in N. micropteryx from the Green River. The occurrence of the derived Pgm-A (A) in a heterozygous condition from two specimens of N. photogenis from the E. Fk. White River sample is speculated to have resulted from hybridization with N. percobromus in this river.

ADDITIONAL PHYLOGENETICALLY INFORMATIVE LOCI

For eight enzyme systems (sAat-A, mAcon, sAp-A, Ck-A, Est-1, G6pdh-A, Pk-A, and Pnp-A) some or all populations of the N. rubellus group, N. stiltius, and N. atherinoides shared one or more derived alleles relative to the distant outgroup N. photogenis. Rare and derived alleles existed at sAat-A, Ck-A, Est-1, and Pnp-A; rare and plesiomorphic alleles existed at sAat-A, mAcon-A, and Pk-A. These alleles were either unique to populations or were found in geographically disjunct samples and provided limited phylogenetic information. Unusual occurrences of atypical alleles at Ck-A, sMdh-B, aMan, and Pgm-A in either N. percobromus or N. photogenis from the E. Fk. White River is suspected to have resulted from hybridization in this area.

GENETIC HETEROGENEITY

Significant heterogeneity occurred at 30 of 33 polyallelic loci for the combined 33 samples of the ingroup (X² = 12847.14, 1984 df, P < 0.01). All loci contributed significantly to this measure of differentiation except sAat-A, Acon-A, and Ck-B. Allelic heterogeneity due to geographic isolation among these 33 samples was also extremely high (Table 2 comparison 1; Fst = 0.634).

For nearly all genetic comparisons of samples within and between ingroup species, the mean within sample variation across all polyallelic loci, Fst was not substantial (Table 2). The positive mean Fst values and their departure from 0 indicates a deficiency of heterozygotes at some loci, an observation not unexpected given that most comparisons were made between groupings of populations or between species across drainage divides.

Most genetic variation occurred as a result of within and among species subdivision, as evidenced by significant genetic heterogeneity measures and the high Fst and FST values calculated. All two or more composite species comparisons (Table 2; comparisons 1-7, 20-26, 28, 30, 32, 34, 41-43) suggested very high subdivision among samples and genetic divergence (Fst = 0.539-0.685; FST = 0.476-0.634). Exceptions included comparisons involving N. rubellus with one or more geographically adjacent populations of N. micropteryx from the Green River and/or N. percobromus from the Wabash River (Table 2; 10-17). The highest level of genetic heterogeneity and divergence occurred for a composite of all members of the N. rubellus group (Table 2; comparison 1). Lower levels of mean genetic heterogeneity, as measured by Fst and FST indices, were not observed until populations or groups of populations for individual species were treated as natural groups (cf. lineages as evidenced by phylogenetic relationships in this study; Table 2; 8, 18, 27, and 44). Genetic heterogeneity, however, still remained relatively high for the widespread N. percobromus (Table 2; 27) and the geographically restricted N. suttkusi (Table 2; 44). In the former species, the systematic elimination of populations being compared, in general accord with their phylogenetic relationships determined in this study (see below), resulted in continued reduction in levels of genetic heterogeneity (Table 2; 27 versus 29, 31, 33, 35-40), further verifying significant divergence and geographic subdivision within this taxon.

PHYLOGENETIC HYPOTHESES

Distance Wagner Analysis.—The six distance measures used in combination with distance Wagner analysis resulted in six different topologies (Fig. 3). Some clades were consistently resolved with identical sister group relationships. (1) Notropis suttkusi and N. percobromus from the

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<td>23. N. rubellus complex without N. micropteryx (TN, CU), N. sp., &amp; N. suttkusi</td>
<td>0.131</td>
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<tr>
<td>24. N. rubellus (LM), N. percobromus, &amp; N. suttkusi</td>
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</tr>
<tr>
<td>25. N. rubellus (LM) &amp; N. percobromus</td>
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<tr>
<td>26. N. percobromus &amp; N. suttkusi</td>
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<td>27. N. percobromus</td>
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<tr>
<td>Taxa and populations compared</td>
<td>Mean value across all polymorphic loci</td>
</tr>
<tr>
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<td>$F_{ST}$</td>
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<tr>
<td>28. <em>N. percobromus</em> without UW &amp; <em>N. suttkusi</em></td>
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</tr>
<tr>
<td>29. <em>N. percobromus</em> without UW</td>
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</tr>
<tr>
<td>30. <em>N. percobromus</em> without UW &amp; IL &amp; <em>N. suttkusi</em></td>
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<tr>
<td>31. <em>N. percobromus</em> without UW &amp; IL</td>
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</tr>
<tr>
<td>32. <em>N. percobromus</em> without UW, IL, &amp; LW &amp; <em>N. suttkusi</em></td>
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<tr>
<td>33. <em>N. percobromus</em> without UW, IL, &amp; LW</td>
<td>0.156</td>
</tr>
<tr>
<td>34. <em>N. percobromus</em> without UW, IL, LW, &amp; UM &amp; <em>N. suttkusi</em></td>
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<tr>
<td>35. <em>N. percobromus</em> without UW, IL, LW, &amp; UM</td>
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<tr>
<td>36. <em>N. percobromus</em> (Ozark Highlands)</td>
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<td>37. <em>N. percobromus</em> (Northern Ozarks)</td>
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<td>38. <em>N. percobromus</em> (Northern Ozarks without MM)</td>
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<td>39. <em>N. percobromus</em> (Northern Ozarks without MM &amp; GA)</td>
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<td>40. <em>N. percobromus</em> (Southern Ozarks &amp; MM)</td>
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<td>42. <em>N. percobromus</em> (AR &amp; OU) &amp; <em>N. suttkusi</em></td>
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<td>43. <em>N. percobromus</em> (OU) &amp; <em>N. suttkusi</em></td>
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<td>44. <em>N. suttkusi</em></td>
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</table>
Interior Highlands always formed a monophyletic group; in some trees this clade also included *N. percobromus* from the upper Mississippi River. Within this clade *N. percobromus* from the Kansas, Osage, Gasconade, and Meramec rivers consistently formed a monophyletic group sister to a clade inclusive of samples from the Arkansas, Black, and White rivers. This Interior Highland clade either formed the sister group to the upper Mississippi River sample (Fig. 3A-D) or to a monophyletic group inclusive of *N. percobromus* from the Ouachita River plus *N. suttkusi* (Fig. 3E-F). In both of the latter trees *N. percobromus* from the upper Mississippi River formed the sister group to the entire Interior Highland clade, inclusive of *N. suttkusi*. (2) *Notropis micropteryx* from the Green, Cumberland, and Tennessee rivers formed a monophyletic group in two trees; this clade included *N. sp.* (New River) in four trees (Fig. 3A-D), whereas in two trees *N. sp.* formed the sister group to all other members of the *N. rubellus* group (Fig. 3E, F). When included in the Eastern Highland clade, *N. sp.* (New River) consistently formed the sister group to a Cumberland-Tennessee clade of *N. micropteryx*; otherwise *N. micropteryx* from the Green River formed the sister group to the Cumberland-Tennessee river clade. (3) *Notropis micropteryx* from the Cumberland River always formed a monophyletic group (Stones River plus Harpeth River). (4) *Notropis rubellus* samples from the Atlantic Slope drainages always formed a monophyletic group (Susquehanna River plus James River).

Other geographic samples from members of the *N. rubellus* group differed in distance Wagner analyses with respect to their sister group relationships depending upon the distance measure used. Of the six different trees, however, the topologies could be grouped into two general classes based primarily on the sister group relationships of *N. rubellus* from tributaries of the upper Ohio River [exclusive of *N. sp.* (New R.)] and samples from rivers of the glaciated Central Lowlands (*N. rubellus* from Lake Michigan; *N. percobromus* from the upper Wabash, Illinois, and upper Mississippi rivers). In four trees (Fig. 3A-D) these samples formed a closer sister group relationship to *N. micropteryx*, while in two trees (Fig. 3E-F) they were more closely related to a clade endemic to rivers of the Interior Highlands (*N. percobromus* and *N. suttkusi*).

Trees generated using Modified Rogers and CS&E arc distances were characterized by nearly identical topologies (Fig. 3A, B), except for relationships among samples of *N. micropteryx* from the Tennessee River and *N. rubellus* from the upper Ohio River, respectively. In these trees an Interior Highland clade of *N. percobromus* and *N. suttkusi* included *N. percobromus* from the upper Mississippi River; this entire clade was sister to a monophyletic group inclusive of remaining members of the *N. rubellus* group. Relationships within the latter clade were similar (Fig. 3A, B), except with respect to relationships within *N. micropteryx* and within *N. rubellus* from the upper Ohio River.

Trees generated using CS&E chord and Edwards E showed close similarity to one another (Fig. 3C, D) and to those using CS&E arc and Modified Rogers (Fig. 3A, B). The CS&E chord and Edwards E trees identified a clade containing *N. rubellus* from the Atlantic Slope and upper Ohio and *N. percobromus* from the middle Wabash river; a sister group relationship between *N. rubellus* from Lake Michigan and *N. percobromus* from the upper Wabash and Illinois rivers, and a clade inclusive of *N. sp.* (New R.) and *N. micropteryx*; and placed *N. rubellus* from the Licking River either as the sister group to the latter more inclusive clade or sister to *N. sp.* (New River) plus *N. micropteryx*. In all four trees *N. percobromus* from the lower Wabash River formed the basal sister group to all members of the *N. rubellus* group exclusive of *N. suttkusi* and *N. percobromus* from the Interior Highlands. The CS&E chord and Edwards E trees varied with respect to the relationships of *N. micropteryx* populations in the Tennessee River and *N. rubellus* populations within the upper Ohio rivers (Fig. 3C, D).

Wagner trees generated using Rogers and Prevosti distances (Fig. 3E, F) were considerably different from the above trees, but shared nearly identical topologies, differing only with respect to sister group relationships among some populations of *N. micropteryx* from the upper Tennessee River. In both trees a series of samples from the glaciated Central Lowlands Province (*N. percobromus* from the upper Mississippi, lower Wabash, Illinois, and upper Wabash rivers and *N. rubellus* from Lake Michigan) formed relative sister group relationships with a monophyletic *N. percobromus*- *N. suttkusi* Interior Highland clade. This clade formed the sister group to a clade of *N. rubellus* from the middle and upper Ohio River and the Atlantic Slope. *Notropis micropteryx* from the Green, Cumberland, and Tennessee rivers formed the sister group to all of the above samples. In both trees *N. sp.* (New R.) formed the sister group to all other members of the *N. rubellus* species group.

**FREQPARS Analysis.**—A total of 55 topologies depicting genealogical relationships among all samples from the *N. rubellus* species group were evaluated for maximum parsimony using FREQPARS. Topologies evaluated were derived from: FREQPARS (n=1); all distance Wagner trees (n=6); and alternative user-defined trees (n=48). Topologies examined ranged in length from 166.57 to 173.79. FREQPARS tree lengths of the distance Wagner topologies varied from 167.36 (Modified Roger's; Fig. 3A) to 168.75 (CS&E chord; Fig. 3C). The shortest FREQPARS trees resolved were among user-defined topologies (length = 166.57 to 173.79). The shortest tree (Fig. 4A) was topologically most similar to those derived using Rogers and Prevosti distances (Fig. 3E, F). Only one other topology (user defined) had a length less than 167 (166.95).
In the two shortest FREQPARS topologies (Fig. 4) N. sp (New R.) formed the sister group to all other samples. *Notropis micropteryx* from the Green, Cumberland, and Tennessee rivers formed the sister group to a monophyletic group inclusive of *N. rubellus* from the upper Ohio River and Atlantic Slope plus a monophyletic group inclusive of *N. suttkusi* and *N. percobromus* from the glaciated Central Lowlands, the upper Mississippi, and the Interior Highlands. Within the latter clade, *N. percobromus* from the Interior Highlands formed a monophyletic group (inclusive of *N. suttkusi*), but samples from the Ozark Highlands and Ouachita River were paraphyletic with respect to a monophyletic *N. suttkusi* from drainages of the Ouachita Highlands in both shortest FREQPARS trees (Fig. 4).

The Roger's and Prevosti distance Wagner (Fig. 3 E, F) trees were congruent with the shortest FREQPARS tree in the phylogenetic placement of *N. sp* (New R.), *N. percobromus* from the glaciated Central Lowlands, and *N. rubellus* from tributaries of the upper and middle Ohio River and rivers from the Atlantic Slope. Differences between the shortest FREQPARS trees and these distance Wagner trees occurred for some samples from the Interior Highland clade of *N. percobromus* and *N. micropteryx* from the Green, Cumberland, and Tennessee rivers. In distance Wagner trees *N. percobromus* from the Arkansas River formed the sister group to a clade from the Ozarks (Black and White rivers). In both FREQPARS trees the Arkansas sample formed the sister group to *N. percobromus* from the Ouachita River plus *N. suttkusi*.
Within *N. micropteryx*, the shortest FREQPARS tree identified a monophyletic Cumberland-Tennessee river clade sister to the Green River (Fig. 4 A). In common with both Roger’s and Prevosti distance Wagner trees (Fig. 3 E, F), a monophyletic Tennessee River clade was not obtained in the shortest FREQPARS tree (Fig. 4 A). Rather, *N. micropteryx* from the Elk River formed the sister group to those samples from the Cumberland River. Relationships of the upper Tennessee River samples varied among all three trees; these samples were either monophyletic (inclusive of the Duck River) (Fig. 3 E) or were paraphyletic with respect to the Cumberland River clade (Fig. 3 F and 4 A). User-specified FREQPARS topologies congruent with these two distance Wagner trees and other rearrangements of samples from the Green-Cumberland-Tennessee clade (i.e., Duck River) increased tree length (length = 167.48-173.05). The shortest of these rearrangements for the Cumberland-Tennessee river samples was similar to the topology identified by Roger’s distance (Fig. 3 E).

Not all nodes in FREQPARS trees were uniformly supported by anagenetic change. Inspection of the shortest FREQPARS topologies revealed branch lengths less than 1.0 for the monophyly of the upper Ohio-Atlantic Slope clade of *N. rubellus* and some clades within this grouping; all groupings within *N. micropteryx* from the Tennessee and Cumberland rivers; *N. micropteryx* (Green-Cumberland-Tennessee rivers); and *N. rubellus* from Lake Michigan plus *N. percobromus* and *N. suttkusi*. However, alternative, user-defined FREQPARS rearrangements of *N. rubellus* from Lake Michigan and the upper Ohio-Atlantic Slope clade and *N. micropteryx* from Green River with the other, more well-corroborated clades of *N. micropteryx* from the Cumberland and Tennessee rivers and the Central Lowland-interior Highland clade of *N. percobromus* plus *N. suttkusi* resulted in longer trees (length = 167.67-168.18). Furthermore, these alternative topologies all shared similar low branch-length support for these alternative nodes. Collapse of nodes with branch lengths less than 1.0 resolves a basal polytomy within the *N. rubellus* species group for the *N. percobromus*-*N. suttkusi*, *N. rubellus*, and *N. micropteryx* clades (Fig. 4 B).

**Discrete Characters and Parsimony Analysis.**—Because of limited variation within *N. micropteryx* samples from the Tennessee and Cumberland rivers and samples of *N. rubellus* from the upper Ohio River, a reduced taxon data set was produced. This was achieved by combining samples from individual rivers within each of these areas into composite samples of “Tennessee,” “Cumberland,” and “Ohio” rivers that were used in all discrete character parsimony analyses.

Phylogenetic analysis of the reduced taxon data set, for allozyme variation coded as discrete characters (plesiomorphic alleles not coded as present in ingroup) and evaluated using Fitch parsimony (Table 3) yielded 25 equally parsimonious trees (length = 125, CI = 0.675, RI = 0.695). All trees were in general agreement with the shortest FREQPARS tree (Fig. 4 A) and distance Wagner trees resulting from Rogers and Prevosti distances (Fig. 3 E, F). The strict consensus of these trees (Fig. 5 A) substantiates: 1) the distinctiveness of *N. sp.* (New R.); 2) the monophyly of a clade inclusive of *N. micropteryx*, *N. rubellus*, *N. percobromus*, and *N. suttkusi*; 3) the monophyly of *N. micropteryx* from the Cumberland and Tennessee rivers; 4) the sister group relationship of *N. percobromus* from the glaciated Central Lowlands to more western populations from the Interior Highlands; 5) the monophyly of a *N. percobromus*-*N. suttkusi* clade within the Interior Highlands and clades within this geographic area; 6) the monophyly of *N. suttkusi*; and 7) the paraphyly of *N. percobromus* populations relative to *N. suttkusi*.

Within the unresolved portions of this tree, a majority rule consensus tree (50% limit) resolved relationships of *N. percobromus* from the Meramec River, *N. rubellus* from Atlantic Slope rivers, and *N. micropteryx* from the Green river in 60% of the trees (Fig. 5 B). Relationships of samples from the Atlantic Slope, Green River, Lake Michigan, and upper Ohio River were dissimilar to those in the shortest FREQPARS trees.
TABLE 3. DATA MATRIX AND CHARACTER STATES FOR PHYLOGENETIC HYPOTHESES USING FITCH PARSIMONY SUMMARIZED IN CONSENSUS TREE IN FIGURE 4A. Genotype arrays for grouped samples and each locus are provided in Appendix 1. Loci mAat-A, Clk-B, sMdh-A, oMan-A, Tpi-A, and Tpi-B were not included in the analysis either because all alleles in ingroup are shared by outgroup or because variation was restricted to rare alleles in a limited number of populations. Character codes within a transformation follow methods outlined by Mayden and Matson (1992) where plesiomorphic alleles present in outgroups are not coded in ingroup.

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<th>Character Numbers*</th>
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<td>Node</td>
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*Character codes: (1) sAt-A: B=0; A=1. (2) mAcon-A: A=0; B=1. (3) Acs-A: C=0; D=1; D or C,D=2; B or B,C=3; A or A,C=4; B=4; C=4; or A,B=5. (4) AcsA: A=0; D=1; C=2; B,C=3; B=4; C=4; or A,B=5. (5) Acs-A: A=0; C=1; A,C=2. (6) Acs-A: A=0; B=1. (7) Acs-A: A=0. (8) Acs-A: A=0; C=1; B,C=2; D=3; E,F=4; G=5; H=6; I=7; J=8; K=9; L=10; M=11; N=12; O=13; P=14; Q=15; R=16; S=17; T=18; U=19; V=20; W=21; X=22; Y=23; Z=24; AA=25; AB=26; AC=27; AD=28; AE=29; AF=30; AG=31; AH=32; AI=33; AJ=34; AK=35; AL=36; AM=37; AN=38; AO=39; AP=40; AQ=41; AR=42; AS=43; AT=44; AU=45; AV=46; AW=47; AX=48; AY=49; AZ=50; BA=51; BB=52; BC=53; BD=54; BE=55; BF=56; BG=57; BH=58; BI=59; BJ=60; BK=61; BL=62; BM=63; BN=64; BO=65; BP=66; BQ=67; BR=68; BS=69; BT=70; BU=71; BV=72; BW=73; BX=74; BY=75; BZ=76; CA=77; CB=78; CC=79; CD=80; CE=81; CF=82; CG=83; CH=84; CI=85; CJ=86; CK=87; CL=88; CM=89; CN=90; CO=91; CP=92; CQ=93; CR=94; CS=95; CT=96; CU=97; CV=98; CW=99; CX=100; CY=101; CZ=102; DA=103; DB=104; DC=105; DE=106; DF=107; DG=108; DH=109; DI=110; DJ=111; DK=112; DL=113; DM=114; DN=115; DO=116; DP=117; DQ=118; DR=119; DS=120; DT=121; DU=122; DV=123; DW=124; DX=125; DY=126; DZ=127. (8) Allele products: A,B,C,c, sMdh-B(b); Pgm-A(a) in this species are suspected to have resulted from introgressive hybridization with the sympatric population of N. rubellus from E. Fk White River and are not included as characteristic of N. photogenis.
Generalized parsimony analysis of the reduced taxon data set for discrete allozyme characters (Table 4; all alleles coded as present in ingroup) resulted in 11 different topologies. A strict consensus of these trees consistently supported the distinctive N. sp. (New R.) as the sister group to a clade inclusive of N. stilius, N. atherinoides, and other N. rubellus (Fig. 5C). This tree also recognized a clade inclusive of N. suttkusi and N. percobromus populations from the Interior Highlands and upper Mississippi River, sister to a clade inclusive of all other samples. Within the latter clade N. rubellus from the Atlantic Slope formed the sister group to a clade inclusive of N. rubellus from Lake Michigan and the Ohio River plus N. micropteryx from the Green, Cumberland, and Tennessee rivers, plus N. percobromus from the Illinois and Wabash rivers. Within the Interior Highland clade a sister group relationship was resolved between N. percobromus from the Ozarks and N. percobromus from the Ouachita River plus N. suttkusi. A majority rule consensus tree of these topologies is provided in Figure 5D.

Phylogenetic analysis of the reduced taxon data set with “rare” alleles eliminated from samples (Table 5) resulted in more trees and lower resolution using both Fitch and Generalized parsimony. When alleles occurring at a frequency of <0.10 were excluded from samples, Fitch parsimony analysis reached the Maximum Trees setting in PAUP of 5000 trees (length=114, CI=0.719, RI=0.724) thus compromising the search. Consistent among these trees was a sister group relationship between N. sp. (New R.) and a clade of N. stilius and N. atherinoides plus all other members of the N. rubellus group (Fig. 6A). Beyond this, the only consistently resolved portions of the tree was the monophyly of the N. rubellus species group (exclusive of N. sp. (New R.)), and a sister group relationship between the Black and White river populations of N. percobromus. A majority rule consensus of these 5000 trees is presented in Figure 6B. In 55% of these trees N. micropteryx from the Green River forms a monophyletic group with conspecifics from the Cumberland and Tennessee rivers. In 68% of the trees N. percobromus forms a paraphyletic assemblage with respect to N. suttkusi. Within N. percobromus the Ouachita and Arkansas river populations are more closely related to N. suttkusi than to other conspecifics in 79% of trees. Other Ozarkian populations were more closely related to the latter clade in 99% of the trees than they were to N. percobromus from the glaciated Central Lowlands physiographic province. Among the central lowland populations there is a progressive east to west sister group relationship to this Interior Highland clade. This is exhibited by the lower Wabash sister to the
TABLE 4. DATA MATRIX AND CHARACTER STATES FOR PHYLOGENETIC HYPOTHESES USING GENERALIZED PARSIMONY SUMMARIZED IN CONSensus TREE IN FIGURE 4C. Characters coded following Butch (1984) with all alleles included; character codes within a transformation are unique for each combination of alleles at a locus within a population. Generalized parsimony invoked unique stepmatrices for each locus. Genotype arrays for grouped samples and each locus are provided in Appendix 1. Loci mAt-A, Ck-B, sMdh-B, aMan-A, Tpi-A, and Tpi-B were not included in the analysis either because all alleles in ingroup are shared by outgroups or because variation was restricted to rare alleles in a limited number of populations.

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1. Characters: (1) sAtt-A: A=0, B=1. (2) mAcon-A: A=1, B=0. (3) Ap-A: C=0, AD=2, AB=3, BC=5, CD=1, BD=2, AD=2, BC=4, CD=0. (4) Ala-A: C=0, D=0, BC=0, BD=2, AD=2, BC=4. (5) sB-A: C=0, A=1, B=1. (6) sCh-A: B=0, A=1. (7) sCh-A: C=0, CD=2, AB=3, BC=5, CD=0, BD=2, AD=2, BC=4, CD=0. (8) sB-A: C=0, AD=2, BC=5, CD=1, BD=2, AD=2, BC=4, CD=0. (9) sD-A: C=0, AD=2, BC=5, CD=1, BD=2, AD=2, BC=4, CD=0. (10) sD-A: C=0, AD=2, BC=5, CD=1, BD=2, AD=2, BC=4, CD=0. (11) sD-A: C=0, AD=2, BC=5, CD=1, BD=2, AD=2, BC=4, CD=0. (12) sD-A: C=0, AD=2, BC=5, CD=1, BD=2, AD=2, BC=4, CD=0. (13) sD-A: C=0, AD=2, BC=5, CD=1, BD=2, AD=2, BC=4, CD=0. (14) sD-A: C=0, AD=2, BC=5, CD=1, BD=2, AD=2, BC=4, CD=0. (15) sD-A: C=0, AD=2, BC=5, CD=1, BD=2, AD=2, BC=4, CD=0. (16) sD-A: C=0, AD=2, BC=5, CD=1, BD=2, AD=2, BC=4, CD=0. (17) sD-A: C=0, AD=2, BC=5, CD=1, BD=2, AD=2, BC=4, CD=0. (18) sD-A: C=0, AD=2, BC=5, CD=1, BD=2, AD=2, BC=4, CD=0. (19) sD-A: C=0, AD=2, BC=5, CD=1, BD=2, AD=2, BC=4, CD=0. (20) sD-A: C=0, AD=2, BC=5, CD=1, BD=2, AD=2, BC=4, CD=0. (21) sD-A: C=0, AD=2, BC=5, CD=1, BD=2, AD=2, BC=4, CD=0. (22) sD-A: C=0, AD=2, BC=5, CD=1, BD=2, AD=2, BC=4, CD=0. (23) sD-A: C=0, AD=2, BC=5, CD=1, BD=2, AD=2, BC=4, CD=0. (24) sD-A: C=0, AD=2, BC=5, CD=1, BD=2, AD=2, BC=4, CD=0. (25) sD-A: C=0, AD=2, BC=5, CD=1, BD=2, AD=2, BC=4, CD=0.

2. Allelic products sCh-A(c), sMdh-A(b), sPgm-A(a) in this species are suspected to have resulted from hybridization with the syntopic population of N. rubellus from E. Fk. White River and are not included as characteristic of N. photogenis.
Illinois plus the upper Mississippi plus the Interior High-
land clade. The middle and upper Wabash populations
form basally unresolved relationships within the *N.
rubellus-percibromus-micropteryx-suttkusi* clade.

Generalized parsimony of the reduced taxon matrix
with rare alleles eliminated (Table 5) resulted in 432 trees
(length 163). A strict consensus of these trees (Fig. 6C)
retains the identity of *N*. sp. (New R.), supports the mono-
phyly of *N. micropteryx* from the Green, Cumberland, and
Tennessee rivers, and supports the monophyly of a clade
inclusive of *N. rubellus*, *N. percibromus* and *N. suttkusi*
relative to these taxa. Additionally, the two populations of *N.
suttkusi* plus the population of *N. percibromus* from the
Ouachita River are consistently resolved as sister groups.
*Notropis rubellus* from the glaciated Central Lowlands and
the Atlantic Slope are unresolved with respect to *N.
percibromus* and *N. suttkusi*. Within the unresolved por-
tions of this consensus tree, a majority rule tree (50%
limit; Fig. 6D) recognized a sister group relationship be-
tween the upper Wabash and Illinois river populations of
*N. percibromus* in 63% of trees, and resolved the Gascon-
ade River population of *N. percibromus* as the sister taxon
to the Ouachita River sample of *N. percibromus* plus *N.
suttkusi* in 95% of trees.

**Discussion**

Population genetics of samples examined from
throughout the range occupied by members of the
*Notropis rubellus* species group reveal patterns of allozyme
variation confirming a history of isolation and differentia-
tion for these species. These data, together with distance
Wagner, FREQPARS, and PAUP analyses, are evaluated
below as evidence for diversification within this clade.
Patterns of genealogical relationships are also evaluated
relative to their concordance with the known geological
history of rivers inhabited by members of this group.

**Spatial Heterogeneity in Allozymes**

Based on phylogenetic reconstruction of the allozyme
data set, the following loci and derived alleles support an
independent history of isolation and divergence in the *N.
rubellus* species group relative to *N. stilbius* and *N.
atherinoides*: sMdh-B(A), mMdhp- A(C), Mpi-A(A, B, D),
Pgk-A(C), and Pgm-A(A). The highly significant levels of heterogeneity at 29 of 33 polymorphic loci and extremely
high $F_{ST}$ for the collection of populations taxonomically
recognized as *N. rubellus* suggests a historical and continued pattern of restricted gene flow and geographic iso-
lolation within the group. These data in concert with phyloge-
TABLE 5. DATA MATRIX AND CHARACTER STATES FOR PHYLOGENETIC HYPOTHESES USING GENERALIZED PARSIMONY AND AN ALLELE DATA SET WITH RARE ALLELES DELETED. Trees are summarized in Figure 5. Only alleles occurring at a frequency > 0.10 are included in coding; character codes within a transformation are unique for each unique combination of alleles at a locus within a population. Generalized parsimony invoked unique stepmatrices for each locus. Genotype arrays for grouped samples and each locus are provided in Appendix 1. Loci mAm-A, Ck-B, sMe-A, aMan-A, Tpi-A, and Tpi-B were not included in the analysis either because all alleles in ingroup are shared by outgroup or because variation was restricted to rare alleles in a limited number of populations.

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<td>Notropis photogenis</td>
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nentic hypotheses argue that *N. rubellus* is not a single evolutionary lineage or species sensu the Evolutionary Species Concept (Wiley and Mayden 2000a, b, c) and diagnosable species sensu the Phylogenetic Species Concept (Mayden, 1997), and that our current taxonomy is a poor reflection of existing evolutionary diversity within this complex.

Restriction of geographic boundaries to species supported by patterns of allozyme variation, phylogenetic analysis, and previous morphological analyses (C. L. Hubbs, unpubl. data; Humphries and Cashner, 1994) result in the recognition of at least five species in the group: *N. rubellus*, *N. micropteryx*, *N. percobromus*, *N. suttkusi*, and *N. sp.* (New R.). Systematic subdivision of the traditionally recognized *N. rubellus* into these evolutionary entities suggests more realistic levels of genetic heterogeneity, subdivision, and divergence (Table 2). For the entire *N. rubellus* group the calculated level of genetic divergence was extremely high (FST = 0.634; Hartl, 1981).

Even following the elimination of *N. suttkusi* and the distinctive and diagnosable species from the upper New River, levels of divergence remained extremely high for a single species (Table 2; FST comparisons 2-4), indicating significant levels of genetic subdivision among the remaining populations within the *N. rubellus* species group when considered a single evolutionary species.

The restriction of the genetically cohesive and previously recognized species *N. micropteryx* to populations in the Tennessee and Cumberland rivers resulted in a relatively low FST (0.109) for this species, suggesting little genetic divergence throughout these ancient drainages. Merger of shiners from the Green River into *N. micropteryx*, as indicated by some distance Wagner and PAUP trees and the shortest FREQPars trees, resulted in minimal elevation of genetic heterogeneity (Table 2; comparison 18). The elevated heterogeneity and divergence estimates from this merger result primarily from a fixed difference at Cbp-1 (Appendix 1) for *N. micropteryx* from the Green versus Cumberland and Tennessee rivers.

Even after partitioning *N. sp.* (New R.), *N. suttkusi*, and *N. micropteryx* from remaining samples of the *N. rubellus* species group, calculated values of FST remained very high for a single species, lending support to the hypothesis of considerable genetic subdivision among remaining drainages containing *N. rubellus* and *N. percobromus* (Table 2; comparison 23 FST = 0.569). Given observed patterns of derived allozyme variation within remaining populations (especially at loci Acp-A, Ald-A, Cbp-2, Est-2, Cpi-A, Cpi-B, SLcldhA, Ldh-A, SmdhA, MmDhp-A, Pfgk-A, and Pgm-A) and the most parsimonious hypotheses of phylogenetic relationships (especially FREQPars), the Great Lake, upper Ohio River, and Atlantic Slope samples generally formed a cohesive evolutionary unit (= *N. rubellus*) relative to remaining populations inclusive of the Wabash and upper Mississippi rivers and most rivers of the Interior Highlands (= *N. percobromus* exclusive of *N. suttkusi*). The restriction of *N. rubellus* to the former composite of drainages resulted in a notable reduction in FST within this species (FST = 0.284) supporting the hypothesis that these populations formed a more genetically cohesive assemblage of taxa sensu the Cohesion Species Concept (Templeton, 1989) delineating lineage independence.

Despite the separation of *N. percobromus* from *N. rubellus* and other species of this group, FST within *N. percobromus* remained very high (FST = 0.504), indicating substantial genetic subdivision persisting within this species. Systematic evaluation of allelic divergence for nested subgroups within *N. percobromus*, moving east to west and south, as argued by natural groupings from phylogenetic analyses, was accompanied with lowered calculated values of FST (Table 2; 29, 31, 33, 35-40). This partitioning of allozyme variation supports the hypothesis of substantial genetic anagenesis in ancestral forms to natural groupings within this species and that *N. percobromus* is a composite of additional diversity, an observation also supported by earlier morphological studies by C. L. Hubbs. Even within the Ozark Highlands, divergence among samples was very high (Table 2; comparison 36 FST = 0.388); further phylogenetic subdivision within the Ozarks resulted in more moderate levels of genetic divergence (Table 2; comparisons 37-40 FST = 0.208-0.282).

Alternative groupings of populations and/or species other than as outlined above that were suggested by some phylogenetic analyses resulted in marked increases in calculated values of genetic divergence. The inclusion of *N. suttkusi* with *N. percobromus* or even subgroups of *N. percobromus* resulted in very high FST values (Table 2; 26, 28, 30, 32, 34, 41-43). While many phylogenetic analyses grouped *N. percobromus* from the southern Ozark rivers and the Ouachita River with *N. suttkusi*, and all phylogenetic analyses indicated that *N. percobromus* from the Ouachita River was sister to *N. suttkusi*, all estimates of population level divergence indicated substantial diversity between populations within these groupings (Table 2).

**HISTORY OF N. SUTTKUSI AND OUACHITA RIVER N. PERCOBROMUS**

Based on morphological characters and some preliminary data from the present study, Humphries and Cashner (1994) proposed that the Ouachita River sample of *N. percobromus* may be of mixed ancestry involving *N. suttkusi* and *N. percobromus*. While allozyme variation depicted in this study consistently supports the sister group relationships between *N. percobromus* from the Ouachita River and *N. suttkusi*, these data do not support the hypothesis of genetic mixing between these populations. Unique and derived alleles support the independent evolution of these populations and levels of heterozygosity do not reflect former genetic interchange of these species. *Notropis percobromus* from the Ouachita River is substan-
These results suggest that while these populations do
possess derived alleles uniting each with their conspecifics, they are genetically similar to most populations of the
adjacently distributed *N. rubellus*. The slight increase in
genetic divergence within *N. rubellus* when these populations
were included suggests that *N. percobromus* from these rivers may have experienced a former mixing event
involving *N. rubellus* from the Great Lakes or upper Ohio
River. Alternatively the Wabash River has had a more
complex hydrological history than currently known and
both *N. percobromus* and *N. rubellus* inhabit this system
separately or with areas of intergradation, similar to pat-
tterns observed by Warren (1992) for *Lepomis miniatus* and
*L. punctatus*.

While the distribution of plesiomorphic alleles pro-
vides minimal information with respect to gene flow and
ancestry (Mayden and Wood, 1995), the distributions of
plesiomorphic alleles at some loci in the Wabash River
populations were peculiar with respect to the distribution
of derived alleles characteristic of the *N. percobromus-N.
suttkusi* clade and *N. rubellus* from Lake Michigan. Est-
2(B) occurred at low frequency in some samples of *N.
micropteryx* but was essentially diagnostic for *N.
percobromus*, occurring elsewhere only in *N. rubellus*
from the middle Wabash sample of *N. rubellus*. Samples of
*N. percobromus* from the upper and lower Wabash rivers
shared the derived sLdh-A(B, C) alleles with *N. suttkusi*
and other *N. percobromus*, while individuals from the middle Wabash possessed only the plesiomorphic sLdh-
A(D) found in outgroups, *N. rubellus*, *N. micropteryx*, and
*N. sp.* (New R.). The derived sLdh-A(C) allele was diag-
nostic for a clade uniting most *N. percobromus* (including
the lower Wabash River sample) and *N. suttkusi*, but was
absent from the middle and upper Wabash samples as well
as from Illinois River samples of *N. percobromus*. Ldh-A(D)
occurred only in *N. percobromus*, except for samples from
the Ouachita and Wabash rivers, where the plesiomorphic
Ldh-A(C) was fixed. The plesiomorphic Cbp-2(B) was
characteristic of a clade inclusive of *N. suttkusi* and all *N.
percobromus*, except those from the Illinois and Wabash
rivers. *Notropis percobromus* from these latter two drainages
possessed the derived allele Cbp-2(A), shared with *N.
rubellus*, *N. micropteryx*, and *N. sp.* (New R.). Conversely,
the derived allele sMdh-B(A) found in the Wabash River and
other populations of *N. percobromus* was absent from
*N. rubellus* from the Lake Michigan drainage, and the
derived allele sAp-A(A) in *N. rubellus* from Lake Michigan
drainage was lacking from any populations of *N.
percobromus* and was only found at low frequency in some
populations of *N. micropteryx*.

Given the complex array of alleles within the Wabash
River samples, it is important to note that the population
from the middle Wabash River is treated as *N. percobromus*
largely as a matter of convenience pending the acquisi-
This study provided the first evidence for *Notropis rubellus* as a member of the subgenus *Notropis* and not the subgenus *Hydrophlox* as presented in previous studies. Nodes on the tree are supported by derived alleles at the protein loci from this drainage. Given these points it seems that the geographic range of what is understood to be the subgenus *Notropis* includes populations that are much closer affinity with *Notropis percobromus*. Furthermore, this sample and our analysis may have been compromised by the limited sample size from this drainage. Given these points it seems that the Wabash River samples as a whole require additional study on a much finer scale than that provided by this study before their phylogenetic history and taxonomic placement will be adequately understood.

**DIFFERENTIATION BETWEEN THE N. RUBELLUS GROUP AND OUTGROUPS**

Mayden and Matson (1988) and Dowling and Brown (1989) argued, on the basis of allozyme and mtDNA variation, respectively, for monophyly of the *N. rubellus* species group. Dowling and Brown's study examined only *N. rubellus* and *N. photogenis* but identified these taxa as a monophyletic group. Mayden and Matson (1988) identified a close relationship between *N. rubellus*, *N. stiltius*, and *N. atherinoides*, relative to other species of *Notropis* (*sensu stritcto*). The latter study included seven species of the subgenus *Notropis*, but did not include *N. photogenis* (Fig. 7), and several outgroup species representing all major groups thought to exist in the formerly recognized *Notropis* (Mayden, 1989).

Allelic products from five loci support both the monophyly and independent history of the *N. rubellus* species group from its closest extant relatives *N. atherinoides*, and *N. photogenis*. These include the derived alleles sMdh-B(A) (found in one individual of *N. photogenis* in a heterozygous condition due to presumed introgression), Mpi-A(A, B, D), Pgk-A(C), Pgm-A(A), and mMdhp-A(C). Some exceptions, however, in terms of reversals and/or parallel evolution of allelic products, occur in one or more populations within the *N. rubellus* group. *Notropis micropteryx* from the Stones River, *N. sp.* (New R.), and *N. rubellus* from Lake Michigan were fixed for the plesiomorphic allele at sMdh-B(C); derived alleles at Mpi-A and Pgk-A were absent from some geographic samples; and derived alleles at Pgm-A and mMdhp-A were reversed or lost in some populations of the *N. rubellus* group (Appendix 1). The incongruencies at these loci in monophyletic groups supported by allelic products at other loci are interpreted within the context of homoplasies, character reversals, or independent fixation of different alleles once occurring in a polymorphic condition in the ancestor to the *N. rubellus* species group or subsequent ancestral species.

Considering *N. photogenis* as the most distant outgroup to the *N. rubellus* group, allelic products from 15 loci corroborate Mayden and Matson's (1988) and Dowling's (1991) hypothesis of a monophyletic group inclusive of *N. rubellus*, *N. stiltius*, and *N. atherinoides*. Loci and allelic products supporting the shared ancestry for *N. stiltius*, *N. atherinoides*, and the *N. rubellus* group include sAat-A(A), mAcon-A, sAcp-A, C, mk-A(A, C), Pgk-A(C), Cbp-l(A, C), Est-1(C), G6pdh-A(B), sLdhp-B(A), sLdh-A(C), Mpi-A(A, B, D), Pgm-A(A), and mMdhp-A(C). These data support the assignment of derived alleles evolved in shared ancestors of unique evolutionary lineages, *sensu* the Phylogenetic Species Concept as a surrogate concept for the Evolutionary Species Concept *fide* Mayden (1997; 1999). These data
also serve to discriminate segregated patterns of gene flow for identifying species consistent with the Evolutionary Species Concept via the Cohesion Species Concept fide Mayden (1997; 1999). Using *N. photogenis* as the most distant outgroup and *N. stilbius* and *N. atherinoideis* as functional outgroups, patterns of allelic evolution specific to the *N. rubellus* group are discussed below.

Among the 33 polymorphic loci examined, evidence for restricted patterns of gene flow exist that serve to diagnose all species except *N. rubellus* [upper Ohio River drainage (not including New River), Atlantic Slope, and Lake Michigan]. While *N. rubellus* as a whole (as identified herein) possesses derived alleles diagnostic of a monophyletic *N. rubellus* species group, except where noted below, its allelic composition lacks uniquely derived allele products supportive of this species being diagnosable. Exceptions to this are populations from the upper Ohio River and Atlantic Slope that share conspicuous frequency differences from remaining populations of *N. rubellus* at two loci. All of these samples shared the loss of, or very low frequencies of, the derived allele mMdhp-A(A), relative to *N. percobromus* from the lower Ohio and upper Mississippi rivers, *N. rubellus* from Lake Michigan, and *N. micropteryx* (Appendix 1). *Notropis rubellus* from the upper Ohio River also shared high frequencies of the derived allele sMdhp-A(A). This allele or a convergent product occurred only rarely in some populations of *N. micropteryx*, four populations of *N. percobromus*, and *N. rubellus* from Lake Michigan. *Notropis rubellus* from Lake Michigan is most similar to eastern populations in its allelic constitution.

Patterns of allelic evolution reflecting a history of isolation and geographic differentiation were most pronounced in samples representative of *N. sp.* (New R.), *N. percobromus*, *N. micropteryx*, and *N. suttkusi*. Early isolation and genetic differentiation of *N. sp.* from the New River above Kanawaha Falls, West Virginia, was deduced from allelic products at five loci. These include loss of alleles Est-2(E, D), rare and unique Gpi-B(E), fixation of the plesiomorphic mMdhp-A(E), and fixation of the plesiomorphic sMdhp-A(C).

A common history of divergence for *N. micropteryx* within the Green, Cumberland, and Tennessee river systems is supported by their common possession of the derived and rare sAp-A(A) allele, a product also found to be rare in *N. rubellus* from Lake Michigan. Populations of *N. micropteryx* also share the apomorphic loss of Est-2(D), a retained-primitive product shared by close outgroups and all other members of the *N. rubellus* group except *N. percobromus* from the Ozarks and upper Mississippi River. The subsequent divergence of *N. micropteryx* from the Cumberland and Tennessee rivers is evidenced by their common possession of the fixed and derived Cbp-1(A), a product considered derived relative to *N. stilbius* and *N. atherinoideis*, but convergently occurring in the most distant outgroup *N. photogenis*. Samples from these two river systems also share the rare, yet derived, sIchdh-B(C). Divergence of *N. micropteryx* from the Cumberland River is evidenced by their shared possession of the rare sIchdh-A(A) and the unique loss of Ald-A(B), a derived allele within the *N. rubellus* group. No alleles were diagnostic of either a Green or Tennessee river clade.

Within the clade inclusive of *N. percobromus* and *N. suttkusi* allelic evolution corroborates an hypothesis of progressive and hierarchical isolation and differentiation of clades in a north to south direction. The unique and derived sIchdh-A(B) allele was shared by *N. percobromus* from the upper and lower Wabash, Illinois, upper Mississippi, and all Interior Highland rivers and *N. suttkusi*. The unique and derived allele sIchdh-A(C) was also shared by specimens from these drainages, except for those in the middle and lower Wabash and Ouachita rivers where the plesiomorphic sIchdh-A(D) was expressed. With reference to the shortest FREQPARS tree (Fig. 4A), the occurrence of sIchdh-A(D) in the lower Wabash River sample either represents a retained-primitive expression or some genetic continuity with *N. rubellus* from the upper Ohio River. The occurrence of this allele in the Ouachita River population is hypothesized to represent a reversal. *Notropis percobromus* from the Ouachita River possessed the derived allele sIchdh-A(A).

A subsequent history of shared divergence of *N. percobromus* from the lower Wabash, upper Mississippi, and Interior Highland rivers is evidenced at three loci. These samples shared sMdhp-A(C), a derived allele not present in samples from the Illinois or middle and upper Wabash rivers. Concordant with this pattern is the loss of the derived mMdhp-A(B) allele, a product derived for the *N. rubellus* group, and the loss of Est-2(E). Both of these latter products were expressed in samples from the Illinois and upper Wabash rivers, either as retained traits or possibly introduced through drainage connections with the more northern populations in the Great Lakes. A common history of isolation and differentiation of *N. percobromus* from the Illinois, upper Mississippi, and Ozarkian rivers is supported by their shared possession of the derived allele Ldh-A(D), a product occurring in most populations in a polymorphic condition with the plesiomorphic allele Ldh-A(C). This apomorphic allele was subsequently lost in the shared ancestor to *N. percobromus* from the Ouachita Highlands and *N. suttkusi*, as well as all populations in the Wabash River where only the plesiomorphic allele is present.

The frequent occurrence of the apomorphic Gpi-A(B) and the fixation of Cbp-2(B) in *N. percobromus* from the upper Mississippi River and rivers of the Interior Highlands plus *N. suttkusi* argues for a uniquely shared evolutionary history for these now largely disjunct groups of populations. Elsewhere, the Cbp-2(B) product is found only in outgroup species. However, given the shortest tree
for the *N. rubellus* group, the fixed allele Cbp-2(A) is optimized as the ancestral allelic product for all of the *N. rubellus* group. Cbp-2(A) presumably reversed to the Cbp-2(B) product in a shared lineage inclusive of these western populations. The subsequent divergence and isolation of an ancestral form to *N. percobromus* plus *N. suttkusi*, endemic to the Interior Highlands, is supported by allelic products at two loci. These samples were characterized by the fixation of the alleles mMdh-A(B) and Pgm-A(B) and the concomitant loss of alleles mMdh-A(A) and Pgm-A(A) (which only occurs at low frequency in the Osage River), the latter alleles representing the ancestral and apomorphic allelic products for the *N. rubellus* group. A history of independent evolution and divergence of *N. percobromus* from the northern Ozarkian rivers from other members of this western group is supported by their shared possession of the fixed and derived Est-2(B). Among these populations the isolation of the Missouri River drainage samples from the Meramec River (Mississippi R. trib.) was evidenced by their unique possession of the derived Gpi-B(B) allele. Finally, among these samples, the high frequency of the derived allele Acp-A(B) in the Osage and Kansas river populations argues for a more recent history of gene flow in these two western-most tributaries to the Missouri River.

An hypothesis of genetic independence of *N. percobromus* from the Ouachita River and southern Ozarks plus *N. suttkusi* from other western populations of the former species is evidenced by their possession of the fixed Ald-A(C) and the corresponding unique loss of the allele Ald-A(B), an ancestral product for the *N. rubellus* species group. Within this grouping divergence of a common ancestral lineage to *N. percobromus* from the Arkansas (southern-most Ozarkian river) and Ouachita rivers plus *N. suttkusi* is supported by their common possession of the derived allele Acp-A(D). This allele was found to be fixed in most populations from these drainages; a similar product occurring convergently in a single individual from the Osage River.

The independent phyletic history of a shared ancestor to *N. suttkusi* and *N. percobromus* from the Ouachita River is supported by two loci. These samples are fixed for Est-2(D), resulting in the loss of the derived alleles Est-2(A, B) typical of other samples from the Interior Highlands. Fixation of the plesiomorphic Ldh-A(C) was accompanied with the loss of the derived Ldh-A(D), a product also characteristic of other *N. percobromus*. The occurrence of these plesiomorphic alleles in the Ouachita Highlands can be viewed as either retained-primitive alleles from a polyallelic ancestral condition or the result of convergent evolution of a similar electromorph. With reference to the shortest tree, this allelic distribution is optimized as convergent with the plesiomorphic condition. Divergence among these latter populations of *N. percobromus* and *N. suttkusi* is evidenced by a shared fixation of the plesiomorphic Pgk-A(D) in *N. suttkusi*, the fixation of the uniquely derived Pgm-A(D) in *N. suttkusi* from the Kiamichi River, and the apomorphic sLdh-A(A) product in *N. percobromus* from the Ouachita River.

**Phylogenetic Relationships**

Allozyme variation within traditionally recognized *Notropis rubellus*, when interpreted with respect to close outgroup species, is consistent with a history of constrained historical patterns of anagenesis and cladogenesis within the species group. For most taxa and populations a similar history is repeatedly reconstructed with phylogenetic topologies derived from distance Wagner, FREQPARS, and Fitch and Generalized parsimony (PAUP) analyses. However, for *N. micropteryx* from the Green River, *N. rubellus* from the upper Ohio River, Atlantic Slope, and Lake Michigan; and *N. percobromus* from the Wabash and Illinois rivers, relationships to other consistently recognized clades are not uniformly supported in some distance Wagner and/or PAUP analyses. All of these rivers occur in areas in or closely associated with the glaciated Central Lowlands. The divergent relationships observed among these taxa may owe their origins to Pleistocene phenomena.

Nearly all analyses suggest evolutionary histories of the *N. rubellus* species group that support 1) a clade of all species exclusive of *N. sp.* (New R.); 2) a Cumberland-Tennessee clade of *N. micropteryx*; 3) an upper Mississippi River-Interior Highland clade involving *N. percobromus* and *N. suttkusi*; 4) a clade within *N. percobromus* involving northern and southern Ozarkian clades of the species; 5) a monophyletic Ouachita Highland clade inclusive of *N. percobromus* from the Ouachita River and *N. suttkusi*; and 6) a monophyletic *N. suttkusi*. Although relationships among samples within some of these clades vary, these clades are generally supported by all phylogenetic algorithms employed. The sister group relationship between *Notropis micropteryx* from the Cumberland and Tennessee rivers is supported by all analyses; in the shortest FREQPARS trees, two distance Wagner trees, and some discrete character coding trees, *N. micropteryx* from the Green River forms the sister group to this clade. *Notropis percobromus* from the upper Mississippi River is nearly always closely related to conspecifics from western drainages, either as the sister group to an Interior Highland clade (inclusive of *N. suttkusi*) or to all or some of the Ozarkian populations. *Notropis percobromus* from the Missouri and Mississippi (Meramec R.) rivers in the northern Ozarks consistently form a monophyletic group with sister group relationships progressing from the west in the Kansas River to the east in the Meramec River. Southern Ozarkian samples from the Arkansas, White, and Black rivers form the sister group to conspecifics from the northern Ozarks. Alternatively, a White-Black river clade forms the sister group to the northern Ozarks, while the
Arkansas River sample is related to conspecifics and *N. suttkusi* from the Ouachita Highlands. Finally, the sister group relationship between *N. percobromus* from the Ouachita River and *N. suttkusi* from other rivers in the Ouachita Highlands is recognized in all topologies.

While some samples of *N. percobromus* from rivers in the glaciated Central Lowlands, *N. micropteryx* from the Green River, and some samples of *N. rubellus* varied in their phylogenetic associations, general congruence consistent with observed patterns of genetic heterogeneity emerges when all analyses are considered. Though *N. micropteryx* from the Green River is identified as the sister group to conspecifics in the Cumberland and Tennessee rivers in only two of four PAUP analyses derived from discrete character codings, this sister group relationship is also found in two distance Wagner trees and the shortest FREQPARS trees. Similarly, levels of genetic divergence as measured by F-statistics within *N. micropteryx*, inclusive of the Green River, were lower than when this population was considered part of the geographically adjacent *N. rubellus* (Table 2). In some distance Wagner trees and in the generalized parsimony PAUP analysis with rare alleles retained, *N. rubellus* and samples of *N. percobromus* from the Illinois and upper and lower Wabash rivers of the glaciated Central Lowlands formed the sister group to *N. micropteryx*, exclusive of other samples of *N. percobromus* from other upper Mississippi River tributaries and the Interior Highlands. However, in all other PAUP analyses, including those where rare alleles were eliminated, the shortest FREQPARS trees, and the Rogers and Prevosti distance Wagner trees, *N. percobromus* from the glaciated Central Lowlands are most closely related to western conspecifics; and *N. rubellus* is sister to *N. percobromus* plus *N. suttkusi*. While genetic divergence within *N. percobromus* is high when the species includes samples from the Central Lowlands (Table 2; 27), their exclusion from the species results in only moderate reduction of $F_{ST}$ (Table 2; 29, 31, 33, 35), indicating that most divergence within the species is associated with heterogeneity within the Interior Highlands. Furthermore, the inclusion of these samples with those of *N. micropteryx* and/or *N. rubellus*, as an evaluation of possible conspecificity with either of these species as suggested by some phylogenetic analyses, results in equally high levels of divergence within these more inclusive species (Table 2; 11, 13-17). The strongest argument in support of a sister group relationship for *N. percobromus* from the glaciated Central Lowlands, western conspecifics, and *N. suttkusi* as argued in the FREQPARS trees is the occurrence of derived allelic compositions shared by all or most of these populations at six loci (Appendix 1; alleles slcdh-A(B, C), sMdh-A(C), Ldh-A(D), Gpi-A(B), Cbp-2(B), and the loss of mMdhp-A(C)). Alternatively, no derived alleles are uniquely shared between *N. percobromus* from the Central Lowlands, *N. rubellus*, and *N. micropteryx* (Appendix 1).

The variable historical relationships obtained for some populations of *N. micropteryx*, *N. percobromus*, and *N. rubellus* may be reflective of multiple factors, any or all of which may be causally related to limited anagenesis and the retention of plesiomorphic alleles. Possible mechanisms responsible for the ambiguity in relationships include 1) sampling error, 2) inherent operational differences between distance and parsimony methods employed, 3) limited allelic anagenesis resulting in retained ancestral genotypes characterizing populations from rivers in the Central Lowlands, 4) differential lineage sorting of allelic products in putative ancestral members of the group, and 5) dispersal and genetic mixing of divergent forms across present drainage divides prior to, during, or following glaciation. The likelihood of these varied mechanisms or combinations of mechanisms may be evaluated based on observed evidence with respect to allozyme variation, age, and geological history.

Sampling error, in terms of limited sample size of individuals representing a population, combined with particular algorithms used to generate phylogenetic estimates, is a potential source of error in phylogenetic reconstruction (Swoford and Berlocher, 1987). It is unlikely that studies of any wide-ranging species group like *N. rubellus* will discover all allelic variation naturally characteristic of every population, and this study is probably no exception. Within any one geographic area the probability of excluding one or more alleles is greater with smaller samples. The sampling strategy necessarily employed in this broad-scale study may be partly responsible for discrepancies observed in relationships for different samples of *N. percobromus* from the Wabash River, *N. micropteryx* from the Green River, or *N. rubellus*. However, even with elimination of rare alleles for PAUP analyses, the relationships of Central Lowland populations of *N. rubellus* and *N. percobromus* to a clade of *N. suttkusi* and other *N. percobromus* were largely consistent between generalized and Fitch parsimony, FREQPARS, and some distance Wagner analyses. That is, other species/populations retained the same relationships with or without rare alleles eliminated, and there was no support for their relationship to *N. micropteryx*.

Allelic profiles of many populations from the glaciated Central Lowland rivers, especially of those in the Great Lakes and the Ohio River (including middle Wabash, but excluding upper and lower Wabash samples) were generally similar. These populations were characterized as largely deficient of derived alleles typical of any of the consistently recognized eastern and western clades discussed above. Total allelic composition for most of these samples is generally like that of outgroup species and is likely representative of an ancestral genotype for the *N. rubellus* group. Exceptions to this generalization include *N. percobromus* from the Wabash and upper Mississippi rivers (excluding middle Wabash). Notropis percobromus
from the Illinois and upper and lower Wabash rivers were unlike N. micropteryx and N. rubellus from the Great Lakes, upper Ohio River, and Atlantic Slope rivers in possessing derived alleles shared with the upper Mississippi River-Interior Highland clades. However, at other loci these samples were plesiomorphic in allelic profiles. This pattern of limited allelic divergence detected within the phylogenetic history of these samples is particularly noticeable in shortest FREQPARS trees where hypothetical ancestral branch lengths uniting N. rubellus from the Great Lakes and many tributaries of the Ohio River with either N. micropteryx or N. percobromus were relatively short. Thus, some disparities in relationships for N. rubellus may, in part, be the result of its potentially ancient age (basal representative) and its generally plesiomorphic genetic composition.

For any phylogenetic analysis, the potential problems associated with independent lineage sorting of various alleles at a locus should be considered as a viable explanation for ambiguous phylogenetic hypotheses (gene trees versus species trees). Pamilo and Nei (1988) evaluated the theoretical impact of this variable with regard to phylogeny reconstruction and concluded that lineage sorting would only present a problem if the effective population size of the ancestor was infinitely large and if the divergence time was very recent. Otherwise, for relatively old species with normal population sizes, genetic (and morphological) indicators of phylogenetic relationships are believed to be sorted and selected in a fashion conducive to effective phylogeny reconstruction. Unfortunately, for almost all organisms the potential problems associated with lineage sorting are essentially moot; it is impossible to know effective population sizes of ancestral forms, and time since divergence cannot be realistically estimated until a phylogeny has been estimated (excluding cases with excellent fossil documentation). Interestingly, however, lineage sorting is probably not responsible for observed ambiguous relationships. Areas in the phylogeny where potential problems of lineage sorting (ambiguous relationships) might be hypothesized to occur include some of the oldest cladogenetic events in the species group, not the more recent events within the eastern or western clades (where cladogenetic reconstruction is stable). Furthermore, within the N. rubellus species group, some cladogenetic events within this group are consistent with other speciation events for the North American freshwater fish fauna (Mayden, 1988a, b). All of these events predate the Pleistocene glaciation.

Samples with ambiguous relationships include those east of the Mississippi River and inclusive of, but north of, the upper Ohio River, as well as those from rivers of the northern Atlantic Slope. The general impact of the multiple ice sheets that formed in this region during the Pleistocene glaciation surely had an influence on the evolutionary history of members of the N. rubellus species group. The mixing of some gene pools from once distinct or diverging evolutionary forms within this group during advancements and retreats of glacial ice could explain the observed genetic patterns for the samples from the glaciated Central Lowlands. It is well known that glacial ice displaced sediments, rivers, and floras and faunas as far south as, and beyond, the Ohio River. In fact, Dowling and Hoeh (1991) detected evidence from mitochondrial DNA variation that the existing contact zone between Luxilus chrysosteptatus and L. cornutus across central Ohio was as far south as central Kentucky during the Pleistocene. Thus, given the geological history of the eastern rivers, the patterns of glacial advance, and the genetic patterns detected by Dowling and Hoeh (1991) within Luxilus, it is possible that the uniform genetic variability and the ambiguous relationships for N. rubellus from the Great Lakes, Ohio River, and Atlantic Slope populations are, in part, due to a historical mixing of these now geographically separate populations.

Given the above scenario of 1) limited anagenetic variation across N. rubellus from the Great Lakes, Ohio River, and Atlantic Slope, 2) their likely possession of ancestral genotypes, and 3) the geological history of pre- and post-Pleistocene rivers and lakes of the Central Lowlands containing members of the N. rubellus species group, the historical relationships observed for N. rubellus with other consistently recognized monophyletic groups are not surprising. While glacial mixing or the dispersal of populations may not solely explain alternative, basal relationships of N. rubellus, the combined retention of a largely ancestral genotype in this species and minimal anagenesis in the common ancestor of N. rubellus and other descendants would make accurate phylogenetic reconstruction difficult. However, given that the shortest FREQPARS topologies consistently recognized a N. rubellus-percobromus-suttkusi clade, sister to an eastern N. micropteryx clade, and this topology was supported in alternative qualitative parsimony analyses, this hypothesis is tentatively favored over alternatives. The minimal support for the FREQPARS node supporting the monophyly of the N. rubellus-percobromus-suttkusi clade is, at this time, hypothesized to be largely the result of minimal anagenetic change in their common ancestor. Given the phylogenetic and biogeographic history of other fish clades inhabiting these same river systems and known geological histories of these rivers, the favored hypothesis is suspected to be a more accurate reflection of cladogenesis within the N. rubellus species group than that provided by alternate topologies.

**Biogeography**

In a distributional study of Missouri fishes, Pflieger (1971) was one of the first researchers to suggest that there may have existed a widespread, pre-Pleistocene ichthyofauna throughout the Teays-Mississippi and/or Laurentian river
System. *Notropis rubellus*, among other species, was suggested to have either existed throughout this expansive drainage system or "...invaded the Ozark Uplands during the Pleistocene Epoch..." (Pfieger, 1971:341). Ensuing from the incorporation of phylogenetic relationships of several eastern North American fish groups into a more global biogeographic hypothesis, Mayden (1985, 1988a, b) argued that much of the ichthyofauna in the existing Central Highland areas predated the Pleistocene and that present-day distributional patterns are largely remnants of a once more widespread fauna and flora. Based on distributional evidence from fishes and geological formations, the pre-Pleistocene Central Highland area was suggested to include upland areas referred to as the Eastern and Interior Highlands, as well as drainages to the north in the now glaciated Central Lowlands. The northern boundary for this region was largely undetermined because of glacial alteration, but would have at least included the unglaciated regions of northern Illinois and parts of Wisconsin and Iowa in the Mississippi River drainage (Mayden, 1985).

Using the phylogenetic relationships among species and populations from clades of fishes inhabiting portions of the Central Highland areas, Mayden (1988a) summarized the "evolutionary history" of the river systems in an area cladogram more consistent with pre-Pleistocene drainage patterns than with existing drainage connections. This parsimony hypothesis of drainage relationships reflects a summary of the evolutionary histories of the fishes formerly and currently inhabiting these rivers and can be evaluated for its generality using other monophyletic fish groups characteristic of Central Highland rivers. Members of the *N. rubellus* species group are distributed throughout most of the Central Highland region, except rivers of the upper Mobile Basin where the closely related *N. stilbius* is endemic. The evolutionary history of this clade serves as a logical biogeographic unit for "homologous" comparisons of patterns of diversification. Furthermore, because members of this group exist in Central Highland rivers presently not occupied by some of the other seven fish clades, these species offer additional historical resolution formerly not available and an opportunity to test previous hypotheses of drainage relationships.

Patterns of allozyme divergence within the *N. rubellus* species group and their reconstructed phylogenetic relationships are congruent with several aspects of the known drainage history for rivers in the Central Highland areas. The formation of the 7.3 m Kanawaha Falls of the New River has presumably served as a substantial isolating mechanism for the allozymically divergent *N. sp.* in the New River, a biogeographic pattern replicated in groups of fishes found in both the New, Kanawaha, and Ohio rivers (Hocutt et al., 1986). The isolation and divergence of *N. micropteryx* in a Late Tertiary, combined Green-Cumberland-Tennessee river drainage in the Eastern Highlands, as argued by divergent allozyme patterns, *F* st parameters, and phylogenetic relationships, is a biogeographic pattern also replicated by several clades (Burr and Page, 1986; Starnes and Etñler, 1986; Mayden 1987a, b, 1988a, b; Mayden and Matson, 1992). The independent drainage history of the Red River in the Ouachita Highlands is sufficient to explain the evolution of *N. suttkusi* in the Blue, Kiamichi, and Little rivers. The more cosmopolitan species *N. percobromus* and *N. rubellus* are distributed across several drainage divides, including the Appalachian Mountains. Geomorphological structures correlated with the divergence of these species are not readily apparent. Insight into the origins of these species as well as the temporal biogeographic relationships for the *N. rubellus* species group must encompass phylogenetic information and a history of drainages presently and formerly occupied by the clade. Current interpretations of the pre- and post-Pleistocene history of drainage patterns in eastern North America, pertinent to the evolution of this species group, have been reviewed in separate chapters of Hocutt and Wiley (1986) and in Mayden (1987a, b).

At least three observations relevant to divergence in this clade suggest that, for the most part, speciation in the group occurred prior to the Pleistocene glaciation. Contributing elements include 1) general correspondence between phylogenetic relationships of species and the Teays-Mississippi and Laurentian waterways, rather than current drainage patterns; 2) the most recent divergence events in the clade are associated with Wisconsin interglacial periods, the Sangamonian; and 3) potential genetic exchange between *N. rubellus, N. percobromus,* and *N. micropteryx* resulted from glacial sluiceways formed during the Pleistocene.

The most influential river basins associated with the evolution of the *N. rubellus* species group include the Pliocene Teays-Mississippian and Laurentian waterways. While these massive basins were extensively modified by glaciation, ancestor-descendant relationships within the *N. rubellus* species group are more consistent with hypothesized former connections within and among these drainages than with river connections observed today. The combined distributions of the group include all drainages formerly part of these watersheds. Thus, ancestral species would have been widespread in these rivers and speciation events resulting in *N. atherinoides, N. stilbius,* and the ancestor to the *N. rubellus* group must have predated the Pliocene (> 7 MYA).

The oldest cladogenetic event within the *N. rubellus* species group is the divergence of *N. sp.* (New R.), occurring in a headwater tributary of the former Teays River, now a tributary of the upper Ohio River. Correlated with this divergence is Kanawaha Falls, a barrier associated with other cladogenetic events and restricted dispersal in
other fish clades. The inception of the 7.3 m Kanawaha Falls, separating the New and Kanawaha rivers is unknown (Lachner and Jenkins, 1971), although Miller (1968) suggested that it was formed during the first glacial recession but provided no supporting data. McKeown et al. (1984) suggested that the formation of Teays Lake (Hocutt, 1979) during the Nebraskan and Kansan would have isolated Etheostoma variatum from an ancestor to E. kanaawhae plus E. asburni, the latter two species occurring only above the falls. However, this hypothesized vicariant scenario is not supported by their phylogenetic hypothesis. A Pleistocene origin for this cladogenetic event in the N. rubellus group is highly questionable given the observed phylogenetic and distributional patterns of component species. Because N. sp. does not form the sister group to either N. rubellus or N. percobromus (both inhabiting former streams of the Teays River), and other cladogenetic events in the species group are correlated with geomorphic changes occurring well before and during the Pleistocene, the basal divergence of N. sp. suggests that the origin of the Kanawaha Falls may date well into the Pliocene. This speciation event is likely involved a peripheral isolation or microvicariant event from the ancestor to the N. rubellus species group.

Subsequent to the evolution of N. sp. (New R.) the earliest divergence within the group involved N. micropteryx and the ancestor to the N. rubellus-percobromus-suttkusi clade. Correlated with the divergence of N. micropteryx, as observed in most trees, is its pre-Pliocene isolation within the Old Ohio River. Included in this ancestral river was the present-day lower Ohio river and portions of the Cumberland and Tennessee Rivers. The Old Ohio River flowed essentially in its current path and included part of the lower Wabash River and the present Green River. This river flowed independently of the combined Cumberland and Tennessee rivers across southern Illinois, western Kentucky, and southeastern Missouri where they eventually united in northeastern Arkansas. This system was independent of other Teays-Mississippi rivers until its confluence with the Mississippi River near Helena, Arkansas. Thus, the pattern of restricted gene flow observed between N. micropteryx from the Green River and conspecifics in the combined Cumberland and Tennessee rivers, as measured by derived alleles and FST parameters, predated Pleistocene glaciation. The minimal branch length support for the monophyly of N. micropteryx and the potentially unresolved relationships between N. micropteryx from the Green River, conspecifics from the Tennessee and Cumberland rivers, and the N. rubellus-percobromus-suttkusi clade in the ancestral Teays-Mississippi River may be fundamentally related to the fact that throughout the Pliocene all three of these separate river systems flowed independently into the Mississippi Embayment, thus separate, independent isolations and divergences.

Similar phylogenetic and geographic relationships observed within Notropis leuciodus from the Green, Cumberland, and Tennessee rivers suggest that this species and N. micropteryx have shared similar histories in the Eastern Highlands and represent "homologous" biogeographic entities. Interestingly, however, within the Cumberland and Tennessee rivers these two species exhibit dramatic differences in genetic heterogeneity. Essentially no geographically structured patterns of restricted gene flow exist within N. micropteryx, while in N. leuciodus these rivers contain two to three distinct forms (Mayden and Matson, 1992).

The sister taxon to N. micropteryx (the ancestor to the N. rubellus-percobromus-suttkusi clade) would have at the same time occupied the remainder of the Pliocene Teays-Mississippi and Laurentian river complexes. With the impact of the Kansan and Nebraskan glacial advances these river systems were radically altered, especially north of northern Ohio and Indiana where their paths are not known with much certainty. However, given observed levels of genetic heterogeneity, as measured by derived alleles and FST patterns, the Laurentian and upper Teays rivers probably contained preglacial populations of N. rubellus. At the same time the lower Teays River and the upper Mississippi River and its western tributaries contained an ancestral clade to N. percobromus and N. suttkusi in a Western Highlands area. The Teays River headwatered in the present upper Ohio River downstream and, perhaps including, the Salt River (Burr and Warren, 1986). The course of the Teays River from its headwaters to the Mississippi River is controversial, but it may have passed north up to the present Scioto River and westward via the Mahomet Valley (Horberg, 1945; Wayne, 1952; Teller, 1973) where it connected with the upper Mississippi River in north-central Illinois. A proposed alternative route suggests that the river turned south in Indiana and followed the Wabash Valley into the Old Ohio River (Fidlar, 1948). If the latter scenario is correct then a western flowing tributary to the Mississippi River in northern Illinois may have had its headwaters adjacent to the Wabash River in a position similar to the present Illinois River. At the same time, the Pittsburgh River, a southern tributary of the Laurentian River, flowed east to the Atlantic Slope. This river flowed through the existing Great Lakes and also included some of the present-day upper Ohio River and Atlantic Slope headwater tributaries (e.g., Allegheny, Monongahela, Youghiohny, and Susquehanna rivers).

The complexities and uncertainties associated with the drainage history of the lower Teays River, the Wabash River, and portions of the Laurentian River in the Central Lowlands of Illinois and Indiana are partially echoed in an apparently equally complex genetic history for N. percobromus and N. rubellus in this region. The sister group relationship of N. rubellus to N. percobromus plus N. suttkusi, rather than to N. micropteryx, argues for the outlet of the
The Wabash River has had a complex history. The lower Wabash presumably formed the headwaters of the Old Ohio River, while the middle and upper Wabash would have been part of the Teays Rivers. The distribution of derived alleles characteristic of the *Notropis rubellus* clade indicate that the ancestor to these species probably inhabited rivers east to, and including a, river in or near the Wabash Valley. *Notropis rubellus* would have existed north and east of where the upper Wabash had its confluence with the Teays River. That the drainage history of the Wabash River is probably more complicated than previously thought is supported by the observation that *N. percobromus*, not *N. micropteryx*, presently occurs in the lower Wabash River, as one would predict given current hypotheses regarding the Old Ohio River. However, this biogeographic occurrence is not unexpected given that a generalized pattern already exists between the Wabash River and more western Ozarkian rivers for *Fundulus conteratus* and *Percina uranidea* (Mayden, 1985, 1987a, 1988a; Grady et al., 1990). Thus, while the Old Ohio River may have flowed largely in its current path upstream to about Madison, Indiana (Ray, 1974), whether or not this Pliocene river actually included the Wabash River is questionable given these data. Rather, tributaries to the lower Wabash River may have flowed northward as a major tributary to the Teays River until the Pleistocene glaciation.

During early glacial advances, however, the Teays and Wabash river valleys were dramatically altered. At this time, if *N. rubellus* and *N. percobromus* were parapatrically, allopatrically, or alloparapatrically distributed within the Teays River, they may have been forced into sympatry and may have also been sympatric with *N. micropteryx* (cf. Green River) in the headwaters of the Old Ohio River. While the *N. percobromus-suttkusi* clade does possess derived alleles from the Wabash River westward, the distribution of alleles at other loci and general patterns of genic heterogeneity are consistent with the hypothesis of a former genetic exchange between shiners from the Wabash and Green rivers and *N. rubellus* from the Laurentian and possibly upper Teays systems. Faunal mixing in this area is not untenable given that 1) advancing glaciers could have pushed *N. percobromus* in the Teays and its Wabash tributaries south in the Wabash system; 2) that the upper Teays River was likely deflected south through the Wabash Valley when blocked by the Kansan glacial advance; and 3) glacial outwash from the Laurentian River eventually broke through the Mahomet Valley (then containing the lower Teays River) and likely introduced *N. rubellus* into the Wabash and other rivers. Thus, the

peculiar genotypic arrays of primarily plesiomorphic alleles observed within populations of *N. percobromus* from the Wabash and Illinois rivers may accurately reflect the reticulate history of the rivers in and around the Wabash Valley. More intensive sampling of genotypic variation within *N. percobromus* from throughout the Wabash and adjacent rivers will be valuable in evaluating the complex drainage history of this region.

Prior to stream modifications in the Pleistocene, the ancestor to the *N. percobromus-suttkusi* clade would have inhabited the upper Mississippi River and the old western Grand, Missouri, White, Arkansas, and Ouachita rivers that formed independent tributaries to the Old Mississippi River. All of these rivers were at that time considerably smaller than they are today, but their independent connections to the Mississippi River floodplain would have limited the dispersal of species typically associated with high-gradient, clear streams. The headwaters of these rivers existed within the current Interior Highlands and topographically similar upland areas extending as a north-south band east of the Plains River in the south and the Hudson Bay drainage in the north. *Notropis percobromus* or *N. suttkusi* occur today in remnant streams of all of these rivers. This greater Interior Highland region was heavily dissected during the Pleistocene by glacial ice destroying upland areas, debris filling river valleys, and by some headwater advancing rivers becoming significantly larger and creating more expansive floodplains. The net result of these activities created habitats that successfully reinforced the isolation of groups of populations of this widespread ancestor. The long-term isolation of groups of populations within the *N. percobromus-suttkusi* clade is reflected in the restricted and geographically consistent patterns of derived alleles across these rivers, the remarkably high measures of genetic heterogeneity within both species, and patterns of morphological divergence among forms documented in previous (see Pflieger, 1971 and references in Humphries and Cashner, 1994) and current studies (Jones and Mayden, unpubl. data).

Near the close of the Pleistocene, during the Sangamonian interglacial (100,000 YA), the Old Arkansas River enlarged its drainage area by capturing a significant portion of the Plains River and successfully separated the Interior Highlands into the Ouachita and Ozark highlands. This event is correlated with the most apical divergence events supported by all phylogenetic hypotheses in the ancestral *N. percobromus-suttkusi* clade (that is the sister group relationship between *N. percobromus* from the Ouachita River and *N. suttkusi*). Prior to the headwater advance of the Arkansas River, this clade presumably inhabited the Old Ouachita River in the Ouachita Highlands (Mayden, 1985). This common drainage became connected with the Arkansas River when it and the Mississippi River occupied a channel farther to the west in the
Mississippi floodplain. Evidence for a common Old Arkansas-Ouachita River in the southern Interior Highlands is observed in some phylogenetic hypotheses within the *Notropis percobromus-suttkusi* clade and is supported by phylogenetic relationships within several other fish clades (Mayden, 1985, 1988b). The divergence of *N. suttkusi* within the western-most rivers of the Old Ouachita River is correlated with the fracturing of this river by the expansion of the Red River drainage, also occurring at the close of the Pleistocene. The high levels of genetic divergence observed between the isolated populations within *N. suttkusi* and with *N. percobromus* from the Ouachita River may have been initiated prior to the Red River capture, but were surely reinforced later by the unfavorable habitats in this area created in the latter river system.

**MATERIALS EXAMINED**

*Notropis rubellus*: ATLANTIC SLOPE DRAINAGES:
- **James River System**: Virginia, Craig Co., Craig Creek at Co. Rd. 606, 5.5 mi. NE New Castle, 20 Sept. 1987 (UAIC 7962.10).

GREAT LAKES DRAINAGES: Lake Michigan System:
- Michigan, Calhoun Co., St. Josephs River at jct. MI Hwy 60 and 22 Mile Road, 27 July 1987 (UAIC 12261.01).

**OHIO RIVER DRAINAGES**: Licking River System: Bath-Rowan Cos., Licking River at Moore’s Ferry, 30 June 1988 (UAIC 8421.06).
- **Kentucky River System**: Kentucky, Clay Co., Red Bird River, 2.5 mi from Hwy 80 near jct 66, along toll road, 2 Oct. 1987 (UAIC 7972.08).
- **Tylgarts Creek System**: Kentucky, Greenup Co., Tylgarts Creek at jct KY Highway 7 and 784, at Kehoe, 29 June 1988 (UAIC 8417.07).

**Big Sandy River System**: Kentucky, Lawrence Co., Blaine Creek along KY Hwy 32 at Prosperity, 4 mi NE Blaine, 3 Oct. 1987 (UAIC 7974.06).

*Notropis percobromus*: MISSISSIPPI RIVER DRAINAGES:
- **Wabash River System**: Indiana, Fulton Co., Tippecanoe River at Talma, 23 June 1988 (UAIC 8435.05).
- **Indiana, Jackson Co., East Fork White River**, 200 m upstream Interstate 65, 22 June 1988 (UAIC 8420.06).

- **Missouri River Drainage: Gasconade River System**: Missouri, Pulaski Co., Big Piney River at Rt Z along Interstate 44, 20 Oct. 1987 (UAIC 7989.06).

- **Kansas River System**: Kansas, Wabaunsee Co., South Branch Mill Creek, 1 mi S Alma, 18 Oct. 1987 (UAIC 7999.04).
- **Spring River System**: Oklahoma, Ottawa Co., Five Mile Creek, 7.5 mi E of Picher, 19 Oct. 1987 (UAIC 7939.04).
- **Ouachita River Drainage**: Arkansas, Polk Co., Ouachita River at Co. Rd. 76, about 1 mi S of Cherry Hill, 28 March 1991 (UAIC 10068.06).

- **Blue River System**: Arkansas, Johnson Co., Blue River at OK Hwy 99, 0.5 mi N Connerville, 16 Oct. 1987 (UAIC 7964.04). Oklahoma, Johnson Co., Blue River, 0.5 mi E Connerville, 17 Oct. 1987 (UAIC 7965.02).

*Notropis micropteryx*: OHIO RIVER DRAINAGE:
- **Green River Drainage: Barren River System**: Kentucky, Allen Co., Trammel Fork at Old State Road Ford, 1 mi NNE Red Hill, 4 Oct. 1987 (UAIC 7967.05).
- **Little River System**: Tennessee, Blount Co., Little River, 2 mi NW Walland at Old Mill Dam, 24 Sept. 1987 (UAIC 7952.05).
- **Little Pigeon River System**: Tennessee, Sevier Co., Little Pigeon River at Red Bank Road, 5 mi E SEvierville, 24 Sept. 1987 (UAIC 7955.06).
- **Clinch River System**: Virginia, Scott Co., Clinch River at Hwy 58/23 bridge, 23 Sept. 1987 (UAIC 7942.10).

*Notropis sp. (New R.)*: Virginia, Grayson Co., Chestnut
Creek at VA Hwy 97 and Rt 608, N of Galax, 21 Sept. 1987 (UAlC 7961.06). Virginia, Grayson Co., Fox Creek at Hwy 58 crossing, 7 July 1990 (UAlC 9848.05).


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APPENDIX 1. GENOTYPIC DISTRIBUTIONS FOR 33 LOCI (FOUR ADDITIONAL LOCI MONOMORPHIC) FOR THE *Notropis rubellus* SPECIES GROUP AND OUTGROUPS. The number of individuals of each genotype is provided following the colon.

<table>
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<th>Locus</th>
<th>N. sp.</th>
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<th>Cumberland River</th>
<th>L. Tennessee River</th>
<th>M. Tennessee River</th>
<th>U. Tennessee River</th>
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<td></td>
<td></td>
<td>New River</td>
<td></td>
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<td></td>
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<tr>
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<td>AA:10</td>
<td>AA:10</td>
<td>AA:10</td>
<td>AA:10</td>
<td>AA:10</td>
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<td>CC:10</td>
<td>CC:10</td>
<td>AA:01</td>
<td>CC:10</td>
</tr>
<tr>
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<td>BC:04</td>
<td>BC:01</td>
<td>CC:05</td>
<td>CC:01</td>
<td>CC:10</td>
</tr>
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<td>AC:01</td>
<td>CC:10</td>
<td>AC:02</td>
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<td>AC:01</td>
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*Note:* The genotypes are represented as follows: BB:10, AA:10, CC:10, etc., indicating the presence of each allele in the genotype.
### Appendix 1. Genotypic distributions continued.

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<td>Buffalo River (Duck R.)</td>
<td>Elk River</td>
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<td>AB:01</td>
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Appendix 1. Genotypic distributions continued.

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<td>CC:10</td>
<td>AA:07 CC:09</td>
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Appendix 1. Genotypic distributions continued.

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(List continues with additional loci and genotypes...
### Appendix 1. Genotypic distributions continued.

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Appendix 1. Genotypic distributions continued.

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Appendix 1: Genotypic distributions continued.

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