

Historical Relationships of Atlantic Slope River Drainages¹

Eugene G. Maurakis, Science Museum of Virginia, 2500 West Broad Street, Richmond, VA 23220 and University of Richmond, VA 23173 and **Diana L. Lipscomb**, Department of Biological Sciences, George Washington University, Washington, DC 20052

ABSTRACT

An analysis of the historical relationships of 19 river drainages (St. Lawrence to Altamaha) on the Atlantic slope of the Appalachian Mountains was conducted using the shared presence of 124 native species of cyprinid fishes. This analysis resulted in an area cladogram that suggests that the rivers of the southern Atlantic slope were historically connected to the drainage of three southern rivers (Flint, Chattahoochee, and Apalachicola) which drain into the Gulf of Mexico. The mid Atlantic and northern Atlantic slope rivers appear to be historically related in support of earlier hypotheses that the mid-Atlantic region provided a refugium for fishes to disperse to the north following the retreat of the glacier and rising sea levels at the end of the Pleistocene. Methods for testing these conclusions are discussed.

Key Words - Historical Biogeography, Cyprinidae, Atlantic Slope Drainages

INTRODUCTION

Many biogeographers distinguish between two different approaches to analyzing and explaining the distributions of organisms - historical biogeography and ecological biogeography. Although history and ecology are not mutually exclusive, the distinction between the effect of evolutionary (or historical) processes, and physical and biotic factors (ecological) that restrict the distributions of organisms is useful because it divides complex biogeographic issues into manageable questions that can be investigated reasonably using evolutionary or ecological methods. This study represents our first in a series of investigations on historical biogeography of rivers that extend from the Appalachian Mountains to the Atlantic. Ultimately our goal is to infer past geologic events and ancient distribution patterns that may be used to explain current patterns of distribution of aquatic organisms in the rivers of the Appalachians.

Cyprinid fishes (Cyprinidae) in Atlantic Slope river drainages of the Appalachian Mountains lend themselves to such an analysis. These cyprinids are primary freshwater fishes, that is, they are physiologically restricted to freshwater and cannot tolerate saline waters. Consequently, salt water is an effective barrier to the dispersion of these fishes from one drainage to another and similarities in fish fauna from one river to the next must be due to past events such as stream capture, lowland inundation, and previous freshwater connections rather than modern dispersal events. Previous studies of fishes of the Appalachians by Holt (1972), Hocutt et al. (1986), Schmidt (1986), and Swift

¹ Presented in the Appalachian Biogeography Symposium, June 25-29, 1995.

et al. (1986) list occurrences of fishes in the drainages and use overall similarity statistics (=phenetic methods) to identify biogeographically related areas and infer probable routes of dispersal and origin (for review of these methods see Simpson, 1980). While these phenetic methods do provide measures of area similarity, it is not always clear how to interpret the meaning of the similarity measures. First, with a wide choice of similarity coefficients, it is not always clear which is most appropriate (Pielou, 1979; McCoy and Heck, 1987) and the measures are often susceptible to differences in number of species in an area (Cheetham and Hazel, 1969). Second, many in both biogeography and systematics have pointed out that the underlying concept of overall similarity in phenetic methods is unlikely to reveal historical patterns because no distinction is made between shared ancient events and shared recent events (e.g., Nelson and Platnick, 1981; Patterson, 1983). Our objectives are to discuss alternative analyses of cyprinid fishes in streams of the Appalachian drainage systems, suggest hypotheses of historical events, and present future plans for testing these hypotheses.

MATERIALS AND METHODS

The presence or absence of 124 native species of primary freshwater cyprinid fishes (Table 1) were obtained for 19 river drainages on the Atlantic Slope of the Appalachian Mountains (Table 2; Fig. 1) (adapted from Hocutt et al., 1986; Schmidt, 1986; and Swift et al., 1986). No exotic or introduced species were used. The hypothesis of the historical relationships of these river drainages was constructed based on shared species of the native fishes using a method initially proposed by Rosen (1984) which is analogous to determining phylogenetic relationships of organisms by cladistic analysis. In cladistic analysis, organisms are considered to be related if they share unique derived characteristics (synapomorphies). Synapomorphies are distinguished from primitive characters (plesiomorphies) by the fact that plesiomorphies are also present in taxa in groups outside the ones being classified (this is called outgroup comparison). In this biogeographic analysis, river drainages are analogous to organisms being classified and the presence of a cyprinid species is analogous to the presence of a characteristic used as evidence for relatedness. Therefore, river drainages were considered to be historically closely related if they shared unique fish species rather than fish species with a broader range into "outgroup" southern peripheral drainages (Flint, Chattahoochee, and Apalachicola rivers in Georgia, Florida, and Alabama) and western peripheral drainages (Tennessee, Kanawha - both above and below the falls, Monongahela, and Allegheny) (Fig. 1). The computer program hennig86 (Farris, 1988; Lipscomb, 1994) was used to construct the cladogram of rivers using the following options: mhennig86*; bb*;. The relative quality of the results was judged using the consistency index (CI), a measure of the degree to which fish species changes on the cladogram are minimal (see Kluge and Farris, 1969), and the retention index (RI), a measure of the amount of relatedness hypothesized by the presence of the fishes that is not in conflict with the final cladogram (Farris, 1989). Multiple equally fit hypotheses of relationships of the rivers were reevaluated using successive weighting (command xs w in hennig86), a procedure that reanalyses after downweighting data that is in conflict with the initial results (Farris, 1969; Carpenter, 1988).

TABLE 1. List of cyprinid species corresponding to numbers in Table 2.

1. <i>Campostoma anomalum</i>	43. <i>N. ariommus</i>	85. <i>N. pyrrhomelas</i>
2. <i>C. pauciradii</i>	44. <i>N. atherinoides</i>	86. <i>N. roseipinnis</i>
3. <i>Clinostomus elongatus</i>	45. <i>N. baileyi</i>	87. <i>N. rubellus</i>
4. <i>C. funduloides</i>	46. <i>N. bellus</i>	88. <i>N. rubricrocerus</i>
5. <i>Coeusius plumbeus</i>	47. <i>N. bifrenatus</i>	89. <i>N. scabriceps</i>
6. <i>Ericymba buccata</i>	48. <i>N. blennius</i>	90. <i>N. szepticus</i>
7. <i>Exoglossum lauræ</i>	49. <i>N. boops</i>	91. <i>N. semperasper</i>
8. <i>E. maxillingua</i>	50. <i>N. buchanani</i>	92. <i>N. spectrunculus</i>
9. <i>Hemmitremia flamea</i>	51. <i>N. callisema</i>	93. <i>N. spilopterus</i>
10. <i>Hybognathus hayi</i>	52. <i>N. camurus</i>	94. <i>N. stilbius</i>
11. <i>H. hankinsoni</i>	53. <i>N. cerasimus</i>	95. <i>N. stramineus</i>
12. <i>H. nichalis</i>	54. <i>N. chalybaeus</i>	96. <i>N. telescopus</i>
13. <i>H. regius</i>	55. <i>N. chrosomus</i>	97. <i>N. trichroistius</i>
14. <i>Hybopsis aestivalis</i>	56. <i>N. chiliticus</i>	98. <i>N. unbratilis</i>
15. <i>H. amblops</i>	57. <i>N. chloristius</i>	99. <i>N. venustus</i>
16. <i>H. cahni</i>	58. <i>N. chlorocephalus</i>	100. <i>N. volucellus</i>
17. <i>H. dissimilis</i>	59. <i>N. chrysocephalus</i>	101. <i>N. whipplei</i>
18. <i>H. hypsinotus</i>	60. <i>N. coccogenis</i>	102. <i>N. wickliffi</i>
19. <i>H. insignis</i>	61. <i>N. cornutus</i>	103. <i>N. xaemurus</i>
20. <i>H. labrosa</i>	62. <i>N. cummingsae</i>	104. <i>N. zonistius</i>
21. <i>H. monacha</i>	63. <i>N. dorsalis</i>	105. <i>Notropis sp. 1</i>
22. <i>H. rubrifrons</i>	64. <i>N. edwardraneyii</i>	106. <i>N. sp. (Palezone shiner)</i>
23. <i>H. storeriana</i>	65. <i>N. emiliae</i>	107. <i>N. sp. (Sawfin shiner)</i>
24. <i>H. winchelli</i>	66. <i>N. euryzonus</i>	108. <i>Phenacobius crassilabrum</i>
25. <i>H. x-punctata</i>	67. <i>N. funeus</i>	109. <i>P. mirabilis</i>
26. <i>H. zanema</i>	68. <i>N. galacturus</i>	110. <i>P. teretulus</i>
27. <i>H. sp. cf. zanema</i>	69. <i>N. harperi</i>	111. <i>P. uranops</i>
28. <i>Margariscus margarita</i>	70. <i>N. heterodon</i>	112. <i>Phoxinus eos</i>
29. <i>Nocomis biguttatus</i>	71. <i>N. heterolepis</i>	113. <i>P. erythrogaster</i>
30. <i>N. effusus</i>	72. <i>N. hudsonius</i>	114. <i>P. neogaeus</i>
31. <i>N. leptcephalus</i>	73. <i>N. hypselopterus</i>	115. <i>P. oreas</i>
32. <i>N. micropogon</i>	74. <i>N. hypsilepis</i>	116. <i>Pimephales notatus</i>
33. <i>N. platyrhynchus</i>	75. <i>N. leedsi</i>	117. <i>P. promelas</i>
34. <i>N. raneji</i>	76. <i>N. leuciodus</i>	118. <i>P. vigilax</i>
35. <i>Notemigonus crysoleucas</i>	77. <i>N. lirus</i>	119. <i>Rhinichthys atratulus</i>
36. <i>Notropis albeolus</i>	78. <i>N. lutipinnis</i>	120. <i>R. cataractae</i>
37. <i>N. alborus</i>	79. <i>N. maculatus</i>	121. <i>Semotilus atromaculatus</i>
38. <i>N. altipinnis</i>	80. <i>N. mekistocholas</i>	122. <i>S. corporalis</i>
39. <i>N. amnis</i>	81. <i>N. niveus</i>	123. <i>S. lumbee</i>
40. <i>N. amoenus</i>	82. <i>N. petersoni</i>	124. <i>S. thorea tianus</i>
41. <i>N. analostanus</i>	83. <i>N. photogenis</i>	
42. <i>N. ardens</i>	84. <i>N. procne</i>	

RESULTS AND BIOGEOGRAPHIC HYPOTHESES

The initial analysis resulted in 6 trees that were equally fit for the data (CI=0.49; RI=0.73). The number of trees was reduced to one by successive weighting (Fig. 2).

The mid-Atlantic and northern (except for the Restagouche) Atlantic rivers are united by the presence of *Semotilus corporalis*. Although this fish is absent from the Roanoke, Tar and Neuse, they are clearly linked with other mid-Atlantic river systems (see Fig. 2) indicating that *S. corporalis* was secondarily lost from these three rivers.

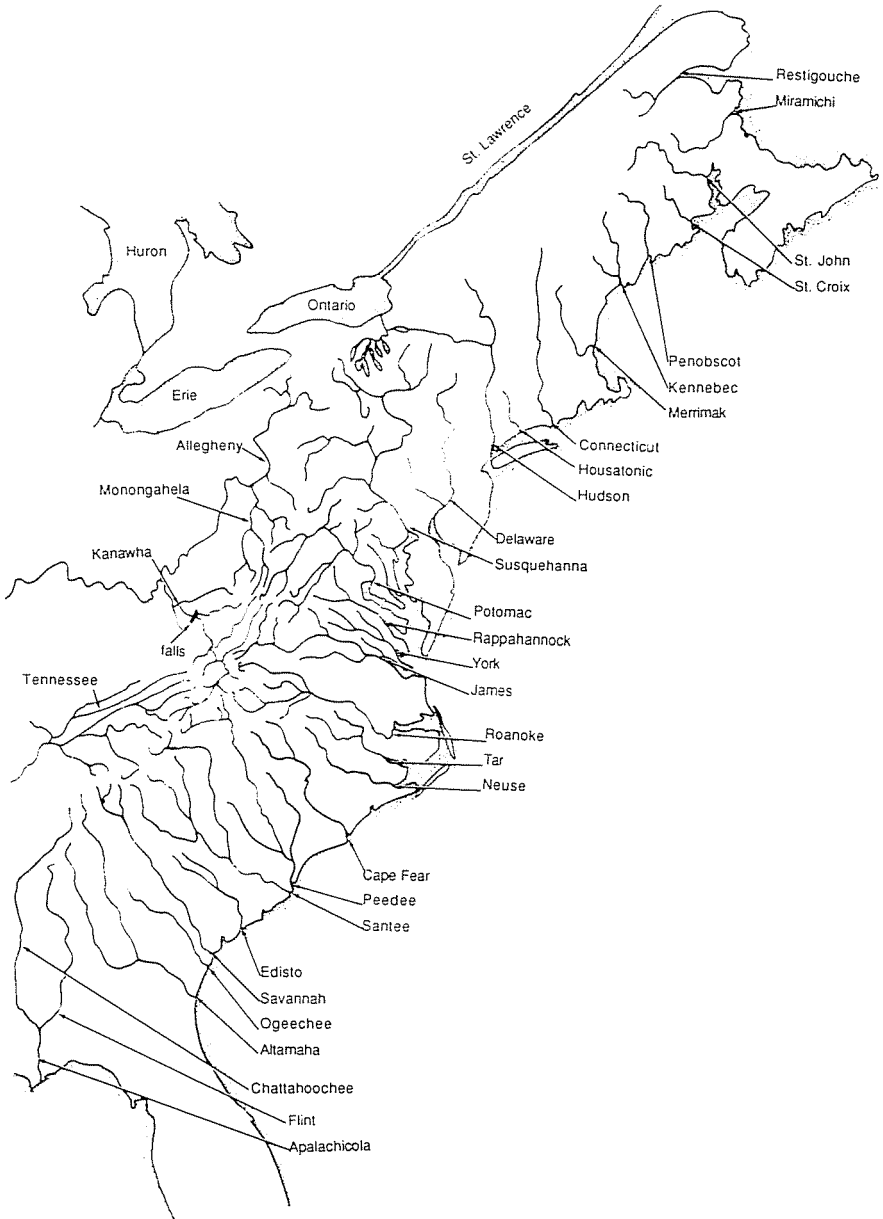


FIGURE 1. The rivers of the Atlantic Slope and the outgroup rivers used in this analysis.

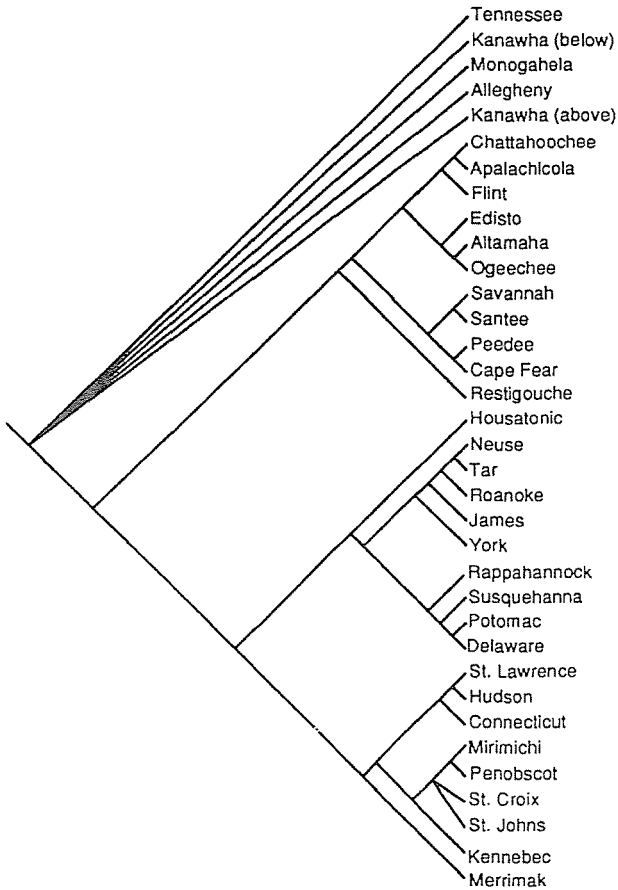


FIGURE 2. The relationships of the Atlantic Slope rivers as revealed by the shared presence of unique species of Cyprinidae.

The northern Appalachian region includes 12 Atlantic coastal drainages from the St. Lawrence River through the Delaware (Fig. 1). Because this region is a natural geologic unit in that all of the rivers drain the northeastern extension of the Appalachian Mountains, it might seem strange that the rivers are not linked into a closely related group (the Penobscot, Merrimack, St. Johns, St. Croix, Kennebec, Mirimichi, Connecticut, Hudson, and St. Lawrence form a unit but are not related in any discernible north-south gradient; and the Housatonic is more closely related to the mid-Atlantic river systems). This distribution can be explained, however, by considering that freshwater fishes were eliminated from the northern Appalachians during the Wisconsinan Ice Age of the Pleistocene because a glacier covered the region. Schmidt (1986) proposed that the present fish fauna of the northern Appalachians is a result of several dispersals from refugia in the mid-Atlantic region as the glacier receded (beginning about 14,700 years ago) (Emery and Garrison, 1967). Our results support this proposal in that the northern rivers are predominately linked to the mid-Atlantic

drainages rather than forming a single isolated lineage on their own. Our study also provides support for the presence of three of the five different refugia proposed by Schmidt (1986) for fishes to populate the northern rivers. The close association between the Housatonic and the mid-Atlantic rivers and the linkage between this group and the rest of the northern Atlantic rivers is consistent with theories for dispersal from both an Atlantic Coastal Plain refugium through widespread interconnecting river channels on the Coastal Plain (see Robb et al., 1981), and an Atlantic Coastal Uplands refugium through stream capture as sea levels rose. The removal of the Restagouche from association with other northern Atlantic rivers may indicate that it was populated from a separate refugium such as the Northeastern Coastal Refugium located off the eastern coast (Howden, 1969; Schmidt, 1986).

The mid-Atlantic rivers are united and form two distinct groups (Susquehanna, Delaware, Potomac, and Rappahannock; and the York, James, Roanoke, Tar, and Neuse). The fauna of all of these rivers was greatly influenced by the glaciers of the Pleistocene. Hocutt et al. (1986) suggest that during that time the lower Susquehanna (now drowned by the Chesapeake Bay) served for exchange of fishes among the Susquehanna, Potomac and Rappahannock rivers. Our results support this idea but indicate a closer relationship among these three rivers than to the York and James which Hocutt et al. (1986) also link to the Susquehanna.

The close relationship of the Neuse, Tar, Roanoke, James and York may be a result of the influence of the now extinct upper Teays river on the Roanoke and James followed by subsequent migration into the other two rivers via stream captures and other drainage modifications that may have existed during lower sea levels of the Pleistocene.

One surprising result of the analysis is the conclusion that the southern Atlantic Slope rivers (Edisto, Altamaha, Ogeechee, Peedee, Cape Fear, Santee, and Savannah) share more recent historical connections with the three rivers that drain into the Gulf of Mexico (Chattahoochee, Flint and Apalachicola) than to the other Atlantic slope rivers. In other words, the southern gulf drainages are not outgroups to the Atlantic slope rivers. The rivers that drain into the gulf are connected and closely related: The Apalachicola drainage rivers contain *Hybopsis winchelli*, *Notropis galacturus*, and *N. venustus*. Southern Atlantic slope drainages (Cape Fear to Altamaha) and the Apalachicola drainage rivers share *Notropis chalybaeus* (lost in the Chattahoochee), *N. hypselopterus* (lost in Cape Fear), *N. maculatus*, and *N. petersoni*. This result supports the hypothesis of Hocutt et al. (1986) that the upper rivers of the gulf drainage (Chattahoochee and Flint) drained into the Atlantic in the Oligocene and may have exchanged fishes with the southern Atlantic slope rivers through interconnecting streams. The two groups of rivers would have been separated later in the Oligocene when sea levels dropped (see Hocutt et al., 1986).

DISCUSSION

Approaches to understanding historical biogeography of a region generally involve two steps: analyzing the pattern of distribution of organisms to develop hypotheses that propose historical explanations for those distributions, followed by testing these hypotheses using either phylogenetic biogeographic methods as described by Brundin (1966; 1992); and/or cladistic biogeographic methods characterized by Nelson and Platnick (1981).

This study represents just the first step. Hypotheses derived here about historical relationships of the Appalachian rivers as suggested by shared fish faunas are consistent with geologic evidence for connections either in the Oligocene (in the case of the southern rivers) and at the end of the Pleistocene (in the case of the mid Atlantic and northern Atlantic rivers). These hypotheses, however, are not without problems. First, it is not clear whether the outgroup rivers were appropriate, which could affect the construction of the cladogram of the rivers (see discussion of rooting problems in Rosen, 1984).

Second, the indications of area similarity from the fish data were not definitive. The relatively low consistency index (CI=48) of the unweighted data indicates that the presence of some cyprinid fishes contributed little to our understanding of river drainage relationships. For example, a few fishes were present in all streams but one (e.g., *Semotilus atromaculatus* is missing from just the Edisto) and don't provide information because they probably represent secondary loss of the fish. Other fishes were missing from all of the Atlantic slope drainages (e.g., *Notropis chrysocephalus*). It isn't clear if the absence of the fishes in the Atlantic slope drainages represents a loss of the common ancient drainage and thus a close relationship of the rivers, or if the presence in the western drainages indicates that they were historically linked. Finally, the distribution of some species is so scattered and disjunct that they do not seem to indicate a coherent pattern except that the fishes made large dispersal jumps or experienced many extinction events in intervening rivers (e.g., *Ericymba buccata*).

Thus, we feel strongly that the hypotheses we outlined above should be tested using phylogenetic or cladistic biogeographic methods. Both of these methods use evolutionary relatedness of organisms to indicate biogeographic relatedness of the areas in which they live. For example, if the Tar and Neuse rivers are historically related then they should contain evolutionarily related fishes as indicated by a cladogram of the fish species. The disadvantages of these tests is the amount of time needed to complete the taxonomic studies and phylogenetic analyses that are required to generate reliable cladograms. We are in the process of testing our hypothesis with cladograms of phylogenetic relationships of species of Percidae [i.e., *Percina (Alvordius)*], and Cyprinidae (species of *Campostoma*, *Clinostomus*, *Exoglossum*, *Hybopsis*, *Nocomis*, *Notropis* (*Cyprinella*, *Luxilus*, and *Lythrus*), and *Semotilus*).

ACKNOWLEDGEMENTS

National Science Foundation Grant DEB-9305925 to D.L.L. is gratefully acknowledged.

LITERATURE CITED

- Brundin, L. 1966. Transantarctic relationships and their significance, as evidenced by chironomid midges, with a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagytia. *Kungliga Svenska Vetenskapssakademiens Handlingar. Fjarde Serien*, 11:1-471.
- Brundin, L. 1992. Phylogenetic biogeography. Pp 343-369, *In* Myers, A.A. and P.S. Giller (eds.). *Analytical Biogeography*. Chapman and Hall, London.
- Carpenter, J.M. 1988. Choosing among equally parsimonious cladograms. *Cladistics*, 4:291-296.

- Cheetham, A. H. and J. E. Hazel. 1969. Binary (presence-absence) similarity coefficients. *Journal of Paleontology*, 43:1130-1136.
- Emery, K. O. and L. E. Garrison. 1967. Sea levels 7,000-20,000 years ago. *Science*, 157:684-687.
- Farris, J. S. 1969. A successive approximations approach to character weighting. *Systematic Zoology* 18:374-385.
- Farris, J. S. 1988. Hennig86 version 1.5 manual. Port Jefferson Station, New York.
- Farris, J. S. 1989. The retention index and the rescaled consistency index. *Cladistics*, 7:1-28.
- Hocutt, R. E. Jenkins and J. R. Stauffer. 1986. Zoogeography of the fishes of the central Appalachians and central Atlantic Coastal Plain. Pp. 161-211, *In* Hocutt, C.H. and E.O. Wiley (eds.). *The Zoogeography of North American Freshwater Fishes*. John Wiley & Sons, New York, NY.
- Holt, P. C (ed.). 1972. The distributional history of the biota of the southern Appalachians (Part III): Vertebrates. Research Division Monograph 4. Virginia Polytechnic Institute and State University. Blacksburg, VA: 43-117.
- Howden, H. F. 1969. Effects of the Pleistocene on North American insects. *Annual Review of Entomology*, 14:39-56.
- Kluge, A. and J.S. Farris. 1969. Quantitative phylogenetics and evolution of the annurans. *Systematic Zoology* 18:1-32.
- Lipscomb, D. L. 1994. Cladistic Analysis Using Hennig86. George Washington University 122 p.
- McCoy, E.D. and K.L. Heck 1987. Some observations on the use of taxonomic similarity in large-scale biogeography. *Journal of Biogeography*, 14:79-87.
- Nelson, G. and N. I. Platnick. 1981. *Systematics and Biogeography: Cladistics and Vicariance*. Columbia University Press, New York. 567p.
- Patterson, C. 1983. Aims and methods in biogeography. *Systematic Association Special Volume*, 23:1-28.
- Pielou, E. C. 1979. *Biogeography*. John Wiley and Sons, New York, NY. 351p.
- Robb, J. M., J. C. Hampson, Jr., and D. C. Twichell. 1981. Geomorphology and sediment stability of a segment of the U.S. continental slope off New Jersey. *Science*, 211:935-937.
- Rosen, D. E. 1984. Hierarchies and history. Pp. 77-97, *In* J.W. Pollard (ed.). *Evolutionary Theory: Paths into the Future*. John Wiley and Sons, New York, NY.
- Schmidt, R. E. 1986. Zoogeography of the northern Appalachians. Pp. 137-159, *In* Hocutt, C.H. and E.O. Wiley (eds.). *The Zoogeography of North American Freshwater Fishes*. John Wiley and Sons, New York, NY.
- Simpson, G. G. 1980. *Why and How: Some Problems and Methods in Historical Biology*. Pergamon Press, Oxford, England 122 p.
- Swift, C. C., G. R. Gilbert, S. A. Bortone, G. H. Burgess, and R. W. Yeger. 1986. Zoogeography of the freshwater fishes of the southeastern United States: Savannah River to Lake Pontchartrain. Pp. 213-265, *In* Hocutt, C.H. and E. O. Wiley (eds.). *The Zoogeography of North American Freshwater Fishes*. John Wiley and Sons, New York, NY.

