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FISHES OF KENTUCKY AND TENNESSEE: A HIERARCHICAL CLASSIFICATION OF DRAINAGES

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ABSTRACT

Our primary objective was to produce a hierarchical classification of the drainages of Kentucky and Tennessee from similarity measures of fish communities inhabiting discrete drainage units. We subdivided river systems of the study region into 60 drainage units, scored presence/absence of 250 fish taxa in each unit, and using Jaccard's index and UPGMA, produced a phenogram of drainage units. Primary clusters were indicative of present-day drainage independence between the Mobile and Mississippi-Ohio basins. Secondary and tertiary clusters indicate two operative distributional determinants: (1) physiography and (2) drainage history. Dichotomy between lowland and upland physiographic divisions (Coastal Plain vs upland regions of the Interior Low and Cumberland plateaus) and to a lesser extent faunal affinities within upland and lowland divisions were apparent. Clustering of units in general accordance with known or hypothesized historical drainage relationships (i.e., pre-Pleistocene drainages) implicates drainage history as a distributional determinant transcending present-day drainage independence and to a large extent physiography. Cases of discordance in our classification with drainage history may reflect effects of multiple faunal interchanges not accompanied by phylogenetic divergence and/or emphasize a need to test the generality of hypothesized drainage reconstructions.

INTRODUCTION

The combined native fish fauna of Kentucky and Tennessee comprises 28.2% (295 species) of the known freshwater fishes in North America. In terms of species density, the two states include the richest ichthyofaunal region on the continent, notably so in the Cumberland and Tennessee river basins (McAllister et al. 1986). Recent syntheses provide unprecedented distributional data and valuable biogeographic interpretations for fishes in each of the two states as well as peripheral regions (e.g., Burr and Page 1986, Burr and Warren 1986, Starnes and Etnier 1986, Etnier and Starnes in press, in Hocutt and Wiley 1986, and Lee et al. 1980). Historical biogeographic analyses, couched in a phylogenetic framework and aimed at explanation of distributions of large-scale continental biotas, have yielded important hypotheses and empirical findings that relate directly to the fish communities of the two states (Wiley and Mayden 1985, Mayden 1988, Grady et al. 1990).

We concur with other biogeographers (Mayden 1987a, Brooks 1988) that ecological and historical biogeography are best viewed as extremes of a continuum of space, time, and form and are not mutually exclusive or philosophically incompatible approaches. We chose in this paper to emphasize the ecological extreme of this continuum (i.e., short temporal and intermediate spatial scales sensu Brooks 1988) because of: (1) the diversity of the fauna; (2) the availability of critically compiled distributional data; (3) the inherent spatial limits imposed by the distributional data; (4) the lack of phylogenetic information for much of the fauna; and (5) the potential for insight compelling unification of historical and ecological biogeographic hypotheses for fish communities of the region.

Our primary objective was to produce a hierarchical classification of the drainages of Kentucky and Tennessee from similarity measures of fish communities as represented by discrete drainage units. We focus interpretation of the classification on ecological or historical factors (and associated hypotheses) that provide general first-order explanations for observed clustering patterns.

METHODS

The study region consists of all drainages lying within the political boundaries of Kentucky and Tennessee and the mainstems of the Ohio and Mississippi rivers adjacent to these states. References to physiographic divisions are based on the simplified physiographic map in Figure 1 (see Burr and Page 1986, Burr and Warren 1986, Starnes and Etnier 1986, Mayden 1987a,b, 1988, Etnier and Starnes in press, and papers cited therein).

We subdivided river systems of the study region into 60 drainage units (Figure 2, Table 1). We delimited most units by physiographic divisions and drainage divides, the presence of waterfalls (i.e., Falls of Ohio, O01 and O06, and Cumberland Falls, C01 and C0¡2), the confluence(s) of

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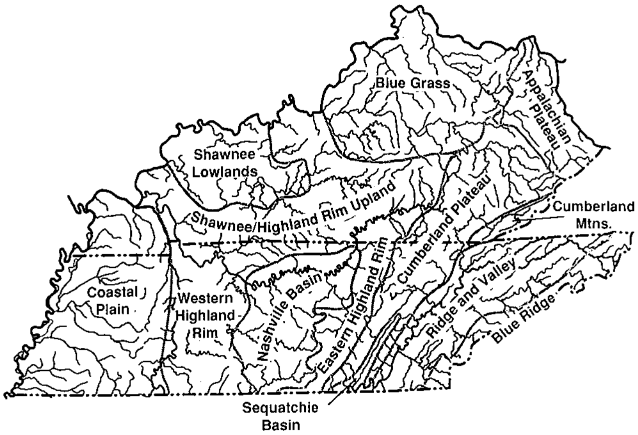

Figure 1. Simplified physiographic map of Kentucky and Tennessee depicting approximate boundaries of major divisions with emphasis on those related to fish distribution.

Table 1. River systems, recognized subsystems, and respective drainage units assessed in Kentucky and Tennessee for fish faunal similarity. Each drainage unit is followed in parentheses by the number of taxa scored as present and as appropriate its designation as a mainstem unit. Drainage unit locations and associated codes are depicted in Figure 3.

River system	Recognized subsystem	Respective drainage units (number of taxa scored)
Cumberland	Upper Cumberland	C01 (28)
		C02 (20)
	Middle Cumberland	C03 (44)
		C04 (61)
		C05 (64; mainstem to Red R.)
		C06 (66)
		C07 (57)
		C08 (55)
		C09 (49)
		C10 (47)
		C11 (52)
	Lower Cumberland	C12 (49)
		C13 (51)
		C14 (46; mainstem below Red R.)
Mobile Basin	Conasauga River	A01 (46)
Mississippi	None	M01 (45; mainstem)
		M02 (33)
		M03 (49)
		M04 (63)
		M05 (52)
		M06 (59)
		M07 (42)
Ohio	"Lower" Ohio	O01 (54; mainstem below Falls of Ohio)
		O02 (29)
		O03 (44)
		O08 (53)
		O09 (40)
		O10 (60)
		O11 (42)

Table 1. (continued)

River system	Recognized subsystem	Respective drainage units (number of taxa scored)
	"Upper" Ohio	O04 (30)
		O05 (36)
		O06 (49; mainstem above Falls of Ohio)
		O07 (53)
		O12 (73)
		O13 (81)
		O14 (53)
		O15 (52)
		O16 (64)
		O17 (61)
		O18 (57)
Tennessee	Upper Tennessee	T01 (49; mainstem to Sequatchie R.)
		T02 (69)
		T03 (67)
		T04 (76)
		T05 (44)
		T06 (64)
		T07 (52)
		T08 (70)
		T09 (46)
		T10 (45)
	"Middle" Tennessee	T11 (67)
		T12 (71)
		T16 (34)
		T17 (93)
	"Lower" Tennessee	T13 (55; southern mainstem to Duck R.)
		T14 (49)
		T15 (34; northern mainstem from Duck R. to mouth)
		T18 (65)
		T19 (54)
		T20 (45)

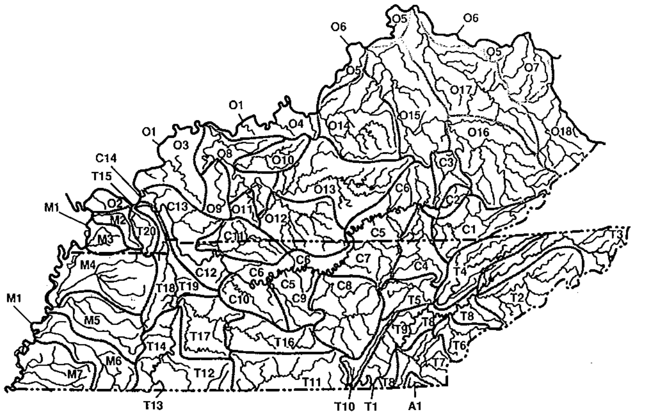

Figure 2. Locations and respective codes of 60 drainage units i Kentucky and Tennessee scored for presence/absence of 250 fis taxa. Drainage systems, recognized subsystems, included drainag units, respective numbers of taxa for each unit, and mainstem unit are given in Table 1. To save space, the number "zero" is eliminate from all units labeled 1-9 (e.g., C01 is C1).

major streams and rivers, and/or peripheral political boundaries of the study area. We subdivided mainstems of the largest rivers (i.e, Mississippi, Ohio, Tennessee, and Cumberland rivers) into separate units delimited by entry/exit points from outside the study region or across boundaries of physiographic divisions. We grouped small, geographically adjacent, direct tributaries to large rivers into separate units (e.g., O04, O05), separate trans-mainstem units (e.g., C06 vs C07, T12 vs T14, T08 vs T09), or units with large tributaries (e.g., C09, C10) (Figure 2).

We scored 250 taxa as present or absent for each of the 60 drainage units (Table 1) using spot distributional maps (Burr and Warren 1986, Etnier and Starnes in press) current through November 1990. Taxa included 223 species, 14 subspecies, and 13 differentiated taxa currently subsumed in species complexes. We excluded from the analysis: known or suspected introductions (exotic or transplanted, sensu Burr and Warren 1986, including widely transplanted game and bait fish); enigmatic records (sensu Burr and Warren 1986); widespread species (e.g., *Semotilus atromaculatus*); and incompletely analyzed species complexes (i.e., the *Campostoma anomalum-oligolepis* complex, the darter subgenus *Doration*, and the *Etheostoma spectabile* complex). A list of taxa included in the study may be obtained from the first author.

Using Jaccard's index, we computed a pairwise similarity matrix of drainage units from the presence/absence data and clustered the units by the unweighted pair-group method using arithmetic averages (UPGMA)(Sneath and Sokal 1973). Analyses were conducted using programs in COMPAH (Boesch 1977).

RESULTS

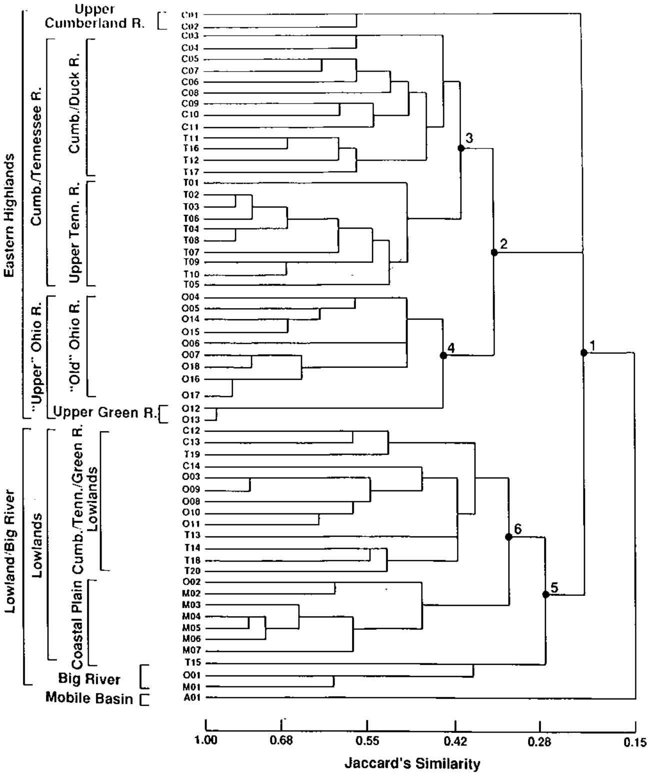

Figure 3. Phenogram of 60 drainage units in Kentucky and Tennessee derived from presence/absence scoring of 250 fish taxa across units. Pairwise drainage unit similarity was estimated with Jaccard's index and clustered using UPGMA. For reference, primary, secondary, tertiary, and terminal hierarchical levels are denoted as node 1; nodes 2 and 5; nodes 3, 4 and 6; and unnumbered nodes, respectively. Bracketed drainage units with descriptive names correspond to geographically depicted clusters in Figures 4-8.

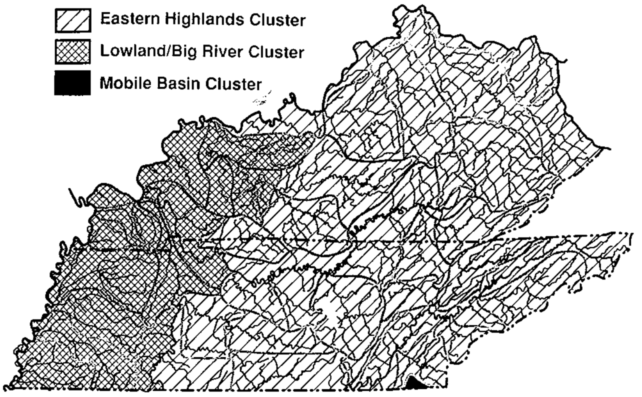

Figure 4. Geographic location of primary level hierarchical clusters (node 1, Figure 3) in Kentucky and Tennessee as derived from presence/absence of 250 fish taxa in 60 drainage units.

Phenetic classification of the 60 drainage units (Figure 3) reveals several levels of hierarchical clusters referred to here as primary, secondary, tertiary, and terminal levels (Figure 3: nodes 1; nodes 2 and 5; nodes 3, 4, and 6; and unnumbered nodes, respectively). The primary level (node 1, Figure 3; Figure 4, Table 1) includes three clusters. The Eastern Highlands cluster represents Upper and "Middle" Tennessee River units, Upper and Middle Cumberland River units, and "Upper" Ohio River units. The Lowland/Big River cluster includes Mississippi, "Lower" Tennessee, "Lower" Ohio, and Lower Cumberland river units. The Mobile Basin cluster represents the Conasauga River unit in southeastern Tennessee. The Upper Cumberland River units (C01 and C02) form a decided outlier within the Eastern Highlands cluster (Figures 3 and 5).

At the secondary level within the Eastern Highlands cluster (node 2, Figure 3; Figure 5), two clusters are formed: (1) Cumberland/Tennessee River and (2) "Upper" Ohio River. The first comprises units of the Middle Cumberland and Upper and "Middle" Tennessee rivers (Table 1). At the tertiary level (node 3, Figure 3; Figure 6), the Cumberland/Tennessee River cluster is divided into a Cumberland/Duck River cluster, comprising units in the Middle Cumberland and "Middle" Tennessee rivers, and

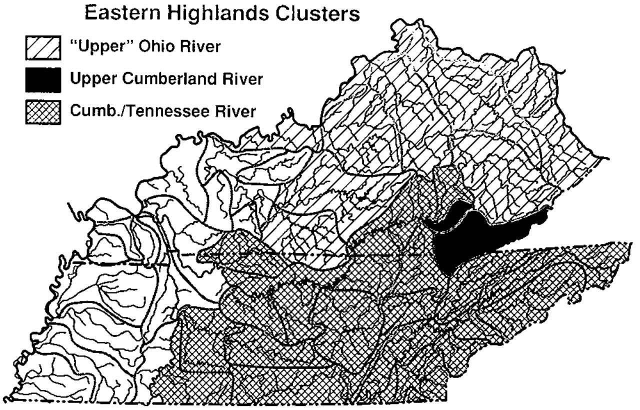

Figure 5. Geographic location of secondary level hierarchical clusters (node 2, Figure 3) and the Upper Cumberland River cluster within the Eastern Highlands cluster of Kentucky and Tennessee as derived from presence/absence of 250 fish taxa in 60 drainage units.

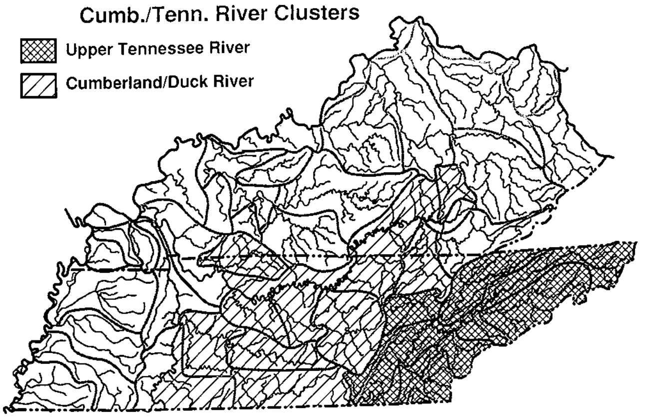

Figure 6. Geographic location of tertiary level hierarchical clusters (node 3, Figure 3) within the Cumberland/Tennessee River cluster of Kentucky and Tennessee as derived from presence/absence of 250 fish taxa in 60 drainage units.

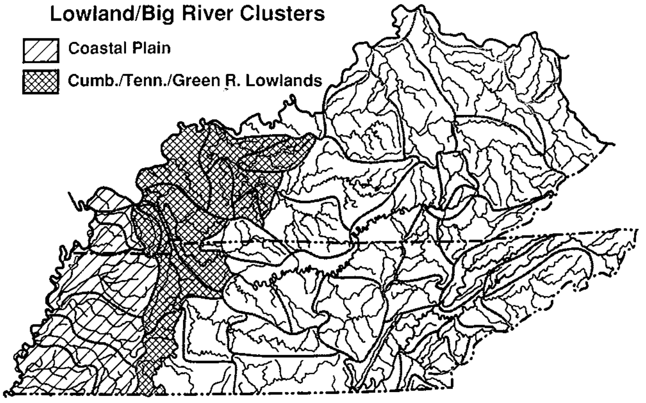

Figure 8. Geographic location of secondary level hierarchical clusters (node 5, Figure 3) within the Lowland/Big River cluster of Kentucky and Tennessee as derived from presence/absence of 250 fish taxa in 60 drainage units.

an Upper Tennessee River cluster, corresponding to Upper Tennessee River units (Table 1). Likewise, the "Upper" Ohio River cluster is divided at the tertiary level (node 4, Figure 3; Figure 7) into an Upper Green (including Barren) River cluster (units O12 and O13, respectively, Figures 2 and 7) and an "Old" Ohio River cluster (units O04-O07 and O14-O18, Figures 2 and 7). The Upper Green River cluster is a relative outlier within the "Upper" Ohio River cluster (Figure 3).

Within the Lowland/Big River cluster, two clusters are formed at the secondary level (node 5, Figure 8). The Big River cluster contains the "Lower" Tennessee River northern mainstem unit (T15, Figure 3, Table 1), "Lower" Ohio River mainstem unit (O01), and Mississippi River mainstem unit (M01). The Lowlands cluster encompasses all units (except the mainstems in the Big River cluster) of the Mississippi, "Lower" Tennessee, and "Lower" Ohio rivers (Figure 3, Table 1). Tertiary level division within the Lowlands cluster (node 6, Figure 3; Figure 8) yields a Coastal Plain cluster of Mississippi River units (except mainstem unit, M01) and a Cumberland/Tennessee/Green River Lowlands cluster of units in the "Lower" Tennessee (except mainstem unit T15) and "Lower" Ohio (except mainstem unit O01) rivers.

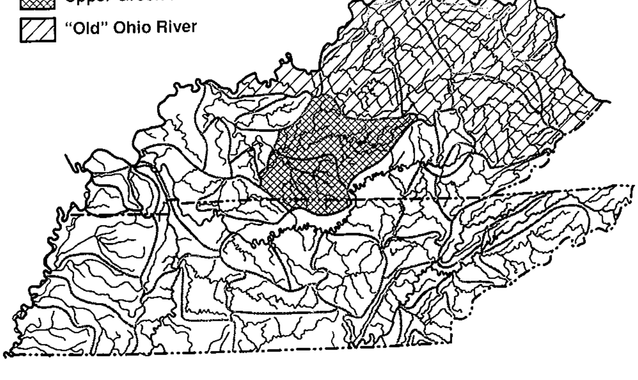

Figure 7. Geographic location of tertiary level hierarchical clusters (node 4, Figure 3) within the "Upper" Ohio River cluster of Kentucky and Tennessee as derived from presence/absence of 250 fish taxa in 60 drainage units.

DISCUSSION

The clustering of drainage units in Kentucky and Tennessee derived from similarity of fish communities implicates several distributional correlates as determinants of spatial patterns: (1) present-day drainage independence; (2) physiography; and (3) drainage history. We acknowledge this categorization is in a broad sense an arbitrary division and an incomplete account of the processes of regional earth history. Even if each is accepted as quasi-independent and the three together are assumed to comprise a reasonably comprehensive list of determinants, we also realize that their relative importance and interactive effects are not readily ascertained if interpretation is confined wholly to the spatiotemporal limits of the data. If viewed from contexts of both historical and ecological biogeographic findings for the study region and beyond, these determinants and associated processes do provide informative foci for discourse. Other works address distributional details (e.g., micro-vicariance via stream capture) and provide interpretations and examples for the biogeography of taxa or groups of taxa in the region (Burr and Page 1986, Burr and Warren 1986, Starnes and Etnier 1986, Etnier and Starnes in press). We make no attempt here to recapitulate nor comprehensively review this information but focus primarily on the classification and general distributional explanations for observed community assemblages.

A possible 'null' hypothesis for our analysis might focus on present-day drainage independence or, from another perspective, the importance of drainage propinquity as a distributional determinant. Under this hypothesis, we would predict that drainage units comprising larger systems (e.g., all Cumberland River units) would cluster together reproducing at successive hierarchical levels the physical interconnectivity of river systems. Such a result is apparent at some proximal hierarchical levels in other phenetic analyses of the fish fauna in the Ohio-Mississippi river valleys (e.g., Burr and Page 1986) and elsewhere (e.g., Swift et al. 1986).

At the primary level, drainage independence is emphasized between Mobile Basin and the remainder of the study region (node 1, Figure 3). The fish fauna of northeastern drainages of Mobile Basin, well represented herein by the fauna of the Conasauga River system (unit A01, Figure 3; Figures 2 and 4), is part of the Central Highlands fauna of North America (Wiley and Mayden 1985, Mayden 1987a, b, 1988). Using seven fish clades in a parsimony analysis of vicariance biogeography of Central Highlands drainages, Mayden (1988) concluded that a large river connection existed between Mobile Basin and the remaining Central (including Eastern and Interior) Highlands. Subsequently, a relatively ancient vicariance event (perhaps break-up of the "Appalachian River") isolated Mobile Basin highlands prior to a sequence of vicariance events within and between the remaining present-day remnants of the highlands (i.e., Eastern and Interior Highlands). Though neither necessary nor sufficient for corroboration of an ancient connection or subsequent vicariance sequence, low similarity of the fish faunas is indicative of the considerable disparity between taxa inhabiting Mobile Basin and the rest of the study region and may imply long-standing independence of the respective areas in spite of shared upland habitat characteristics and adjacent headwaters. Although influence of intradrainage propinquity is apparent at terminal levels (e.g., cluster of units C03-C11 or M03-M07, Figure 3) and given the Mobile Basin case, present-day drainage independence as judged from the classification of drainage units is not the predominant distributional determinant operating within the study region.

A second 'null' hypothesis for the classification might invoke physiography as a distributional determinant. Under this hypothesis, we would predict that drainage unit clusters adhere to natural boundaries of physiographic divisions notwithstanding natural divides (i.e., drainage independence) or intradrainage propinquity. The occurrence (or exclusion) of particular taxa in discrete physiographic divisions is well documented within the study region; numerous examples and probable ecological correlates are discussed elsewhere (Burr and Warren 1986, Starnes and Etnier 1986). Other phenetic analyses of fishes by drainage units also evidence physiographic concordance (e.g., Burr and Warren 1986, Cross et al. 1986, Swift et al. 1986).

Within the constraints imposed by drainage unit boundaries, our classification is concordant with physiographic divisions at several hierarchical levels (Figure 1). For example, at the primary level (node 1, Figure 3; Figure 4), units in the Western Highland Rim physiographic division and divisions east and northeast (i.e., the Eastern Highlands cluster), cluster separately from those in the Coastal Plain, Shawnee Lowlands divisions, and lower reaches of the Tennessee and Cumberland rivers (i.e., the Lowland/Big River cluster). These two clusters underscore a basic dichotomy in physiographic development that translates to extremes in fish habitat types (viz., upland vs lowland) and ultimately to differential composition of faunal assemblages.

The Upper Cumberland River cluster (Figures 3 and 5) provides another example of the effects of physiography (Burr and Warren 1986, Starnes and Etnier 1986). The two units comprising this cluster (C01 and C02) represent the major portion of the Cumberland River draining the Cumberland Plateau. Starnes and Etnier (1986) upon reviewing distributions of individual taxa stated that the profound influence of physiography on distributions of fish species in the upper Cumberland River suggests physiography transcends other distributional determinants. Our classification supports their observation. We emphasize here that physiography and the upstream migration of Cumberland Falls (i.e., drainage history, Starnes and Starnes 1978, Warren 1981, Burr and Warren 1986) likely were interactive in producing present-day faunal distributions. The Falls and its migration influenced faunal composition upstream of the point of origin of Cumberland Falls. Within the region of the migration path of the Falls, the complex physiographic interface of the Cumberland Plateau and Highland Rim (Starnes and Etnier 1986) determined the upstream limits of fish adapted to drainage characteristics of the Highland Rim.

In a less clear-cut example at the tertiary level (node 3, Figure 3; Figure 6), drainage units primarily within the Ridge and Valley/Blue Ridge/Sequatchie Basin physiographic divisions (i.e., the Upper Tennessee River cluster) are clustered separately from those of the Highland Rim/Nashville Basin and part of the Cumberland Plateau (i.e., the Cumberland/Duck River cluster). Allowing here for the occasional confounding of two or more physiographic divisions in a particular drainage unit(s) (e.g., units T02, T03 or T05, T09), the adherence to physiography is striking but nevertheless imperfect. For instance, unit T05 (the Obed River drainage, Figures 1 and 2) lies primarily on the Cumberland Plateau but clustered with the units in the Ridge and Valley/Blue Ridge/Sequatchie Basin divisions, albeit as a relative outlier. Other examples of physiographic influence also are apparent at terminal levels. The cluster of units O03 and O08-O11 (Figure 3), representing the Tradewater and lower Green River systems, conforms to the Shawnee Lowlands physiographic division (Figure 1), and the terminal cluster of units O14 and O15 (Salt and lower Kentucky rivers, respectively) essentially delimits the Bluegrass division.

Cluster patterns also show strong discordance with physiography. The Cumberland/Appalachian Plateau division (Figure 1), for example, does not form a discrete cluster of drainage units. If we accept the physiographic 'null' hypothesis, we must do so only with caution. Namely, interaction with or predominance of other determinants (e.g., historical independence of the Upper Tennessee River or zoogeographic barriers such as Cumberland Falls) may confound drainage unit clusters otherwise concordant with physiography.

Finally, we consider drainage history as a distributional determinant. As noted previously, Mayden (1988) reconstructed the historical drainage relationships of the Central Highlands using vicariance biogeographic methods (see also Wiley and Mayden 1985). To facilitate discussion and integrate Mayden's (1988) findings with our study, we consider here only drainages common to both studies, limiting comparison primarily to the units of the Eastern Highlands and Mobile Basin clusters (Figures 3-5). Mayden (1988) concluded that pre-Pleistocene vicariance events split a pre-existing and widespread Central Highlands fish fauna in a specific temporal sequence producing present-day areas of endemism. The temporal sequence of hypothesized vicariance events is: (1) Mobile Basin (unit A01) vs remaining Central (including Eastern and Interior) Highlands; (2) Salt, Green, Cumberland, Duck, and Tennessee rivers (units O14; O12-O13; T16-T17; and T01-T12, respectively) vs remaining Central (including Eastern and Interior) Highlands; and (3) Kentucky, Licking, and Big Sandy rivers (units O15-O16; O17; and O18, respectively) vs remaining Central (including Interior) Highlands. In most cases, he provided evidence that vicariance was correlative with events in earth history (e.g., event 3 and the break-up of the pre-Pleistocene Teays River). Importantly, Mayden's (1988) results imply that each vicariance event affected not only the fish clades included in his analysis but a significant proportion of the Central Highlands fish community. Independent research using biochemical data from other fish clades supports in large part his conclusions, especially as related to our study region (Grady et al. 1990).

Using this background, a 'null' hypothesis invoking drainage history can be conceptualized. If present-day fish faunal assemblages are primarily products of drainage history, we would predict that drainage units will cluster in groups correlative to vicariance events verified via hypothesized earth history and/or strongly supported by phylogenetic divergence patterns of faunal members. For example, we would expect drainage units of former tributaries of the pre-Pleistocene Teays River (Burr and Page 1986, Burr and Warren 1986, Hocutt et al. 1986) to form a discrete cluster. This particular expectation largely is met in the "Old" Ohio River cluster (Figures 3 and 7). Other exemplars supporting this prediction also are evident in our classification (Figure 3). As discussed previously, the Mobile Basin cluster is quite distinct from the Eastern Highlands cluster suggesting node 1 (Figure 3) as correlative to the earliest vicariance event outlined by Mayden (1988). Within the Eastern Highlands Cluster, the

Cumberland/Tennessee River cluster (Figures 3 and 5) and "Upper" Ohio River cluster (Figures 3 and 5) implicate node 2 (Figure 3) at least in part as correlative to later vicariance events hypothesized by Mayden (1988).

A notable departure between our classification and the drainage relationships resolved by Mayden (1988) is the placement of the Salt River (unit O14, Figure 3) and the "Upper" Green River cluster within the "Upper" Ohio River cluster (Figures 3 and 7). Under Mayden's (1988) hypothesis, the Salt River would be predicted to be more similar to the Cumberland/Tennessee River cluster than the "Old" Ohio River cluster. Interestingly, the geologic evidence for its pre-Pleistocene relationship with either the ancestral Ohio River or Teays River is equivocal (Burr and Warren 1986). In this case, the disparity between our classification and results of vicariance biogeography is enigmatic and questions to some extent the robustness of the classification and/or the generality of hypotheses of historical drainage relationships. Clearly, however, the present-day faunal community in Salt River is most similar to that presently found in former Teays River tributaries and/or the Blue Grass physiographic division.

The Upper Green River cluster forms a terminal-level outlier to the "Old" Ohio River cluster rather than being allied to the Cumberland/Tennessee River cluster, the latter being predicted from phylogenetically derived drainage reconstructions (Mayden 1988). Although consistently allied in parsimonious solutions, Mayden (1988) was unable to resolve relationships among the Green, Cumberland, Duck, and Tennessee rivers. He attributed ambiguities among possible drainage interrelationships to different and independent speciation responses of included clades to a myriad of vicariance and/or dispersal/extinction events. Using analogous reasoning, we suggest that the incongruence between vicariance and phenetic results may reflect real, but temporally and/or spatially, disparate points in the histories of the drainages involved and not simply methodological artifact.

We emphasize, as have others (Cracraft 1988, Mayden 1988), that vicariance biogeography ostensibly records temporal sequences of speciation events, a mostly non-reticulate history, and overlays this sequence on areas (drainages) which in fact may have complex reticulate histories. From the perspective of our methods, reticulation of drainages and their faunas, unaccompanied by phylogenetic divergence, simply increases estimates of similarity among involved drainages, but nevertheless may reflect real, albeit indirectly measured, events in the biogeographic history of that community. Given the likelihood of multiple faunal exchanges among drainages that are unaccompanied by phylogenetic divergence, the points of departure are much less surprising than the high degree of congruence between independently reconstructed drainage histories and similarity measures of present-day fish communities.

Our classification of the drainage units of Kentucky and Tennessee in large part supports previous hypotheses of regional earth history and emphasizes the relative importance of drainage history in structuring and understanding fish faunal assemblages. The classification is much less informative without reference to longer temporal and larger spatial scales; a result that underscores effects of scaling and the inherent nature of biogeography as a continuum (Brooks 1988). The classification results also highlight the need to test the level of generality of current hypotheses of drainage histories via phylogenetic analysis of other endemic fish clades. In particular the relationships of the Salt and Upper Green rivers to the remainder of the Ohio River valley may be more complex than phenetic or vicariance methods thus far indicate. Although transcended by drainage history to a large degree, physiography, especially the dichotomy between upland and lowland drainage units, is an important determinant of similarity in faunal composition among drainage units, both within and among major river systems. We conclude that the classification implicates drainage history and physiography, considered singly and/or interactively, as the primary distributional determinants of fishes in Kentucky and Tennessee.

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LITERATURE CITED

Boesch, D. F. 1977. Application of numerical classification in ecological investigations of water pollution. Special Scientific Report No. 77, Virginia Institute of Marine Science, EPA-600/3-77-033.

Brooks, D. R. 1988. Scaling effects in biogeography: a new view of space, time, and form. Syst. Zool. 37:237-244.

Burr, B. M., and L. M. Page. 1986. Zoogeography of the fishes of the lower Ohio-upper Mississippi River Basin. Pp. 287-424 in: Hocutt, C.H., and E.O. Wiley (eds.). The zoogeography of North American freshwater fishes. John Wiley and Sons, Inc., NY.

Burr, B.M., and M.L. Warren, Jr. 1986. A distributional atlas of Kentucky fishes. Kentucky Nature Preserves Commission Scientific and Technical Series No. 4.

Cracraft, J. 1988. Deep-history biogeography: retrieving the historical pattern of evolving continental biotas. Syst. Zool. 37:221-236.

Cross, F. B., R. L. Mayden, and J. D. Stewart. 1986. Fishes in the western Mississippi Basin (Missouri, Arkansas and Red rivers). Pp. 363-412 *in*: Hocutt, C. H., and E. O. Wiley (eds.). The zoogeography of North American freshwater fishes. John Wiley and Sons, Inc., NY.

Etnier, D. A., and W. C. Starnes. In press. The fishes of Tennessee. University of Tennessee Press, Knoxville.

Grady, J. M., R. C. Cashner, and J. S. Rogers. 1990. Evolutionary and biogeographic relationships of *Fundulus catenatus* (Fundulidae). Copeia 1990:315-323.

Hocutt, C. H. and E. O. Wiley (eds.). 1986. The zoogeography of North American freshwater fishes. John Wiley and Sons, Inc., NY.

Hocutt, C. H., R. E. Jenkins, and J. R. Stauffer, Jr. 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 and Sons, Inc., NY.

Lee, D. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer, Jr. (eds.) 1980 et seq. Atlas of North American freshwater fishes. North Carolina State Museum of Natural History, Raleigh.

Mayden, R. L. 1987a. Pleistocene glaciation and historical biogeography of North American central-highland fishes. Pp. 141-151 *in*: Johnson, W. C. (ed.). Quaternary environments of Kansas. Kansas Geological Survey, Guidebook Series 5.

Mayden, R. L. 1987b. Historical ecology and North American highland fishes: a research program in community ecology. Pp. 210-222 *in*: Matthews, W. J., and D. C. Heins (eds.). Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Mayden, R. L. 1988. Vicariance biogeography, parsimony, and evolution in North American freshwater fishes. Syst. Zool. 37:329-355.

McAllister, D. E., S. P. Platania, F. W. Schueler, M. E. Baldwin, and D. S. Lee. 1986. Ichthyofaunal patterns on a geographic grid. Pp. 17-51 *in*: Hocutt, C. H., and E. O. Wiley (eds.). The zoogeography of North American freshwater fishes. John Wiley and Sons, Inc., NY.

Sneath, P. H. A. and R. R. Sokal. 1973. Numerical taxonomy. W. H. Freeman and Co., San Francisco, CA.

Starnes, W. C., and D. A. Etnier. 1986. Drainage evolution and fish biogeography of the Tennessee and Cumberland rivers drainage realm. Pp. 325-361 *in*: Hocutt, C. H., and E. O. Wiley (eds.). The zoogeography of North American freshwater fishes. John Wiley and Sons, Inc., NY.

Starnes, W. C., and L. B. Starnes. 1978. A new cyprinid of the genus *Phoxinus* endemic to the upper Cumberland River drainage. Copeia 1978:508-516.

Swift, C. C., C. R. Gilbert, S. A. Bortone, G. H. Burgess, and R. W. Yerger. 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, Inc., NY.

Warren, M. L., Jr. 1981. New distributional records of eastern Kentucky fishes. Brimleyana 6:129-140.

Wiley, E. O., and R. L. Mayden. 1985. Species and speciation in phylogenetic systematics, with examples from the North American fish fauna. Ann. Mo. Bot. Gard. 72:596-635.