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ORIGINAL ARTICLE

A hierarchical classification of freshwater mussel diversity in North America

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ABSTRACT

Aim North America harbours the most diverse freshwater mussel fauna on Earth. This fauna has high endemism at the continental scale and within individual river systems. Previous faunal classifications for North America were based on intuitive, subjective assessments of species distributions, primarily the occurrence of endemic species, and do not portray continent-wide patterns of faunal similarity. The aim of this study is to provide an analytical portrayal of patterns of mussel diversity in a hierarchical framework that informs the biogeographical history of the fauna.

Location The study considered the mussel fauna of North America from the Rio Grande system northwards.

Methods Patterns of mussel faunal similarity in 126 river systems or lake watersheds across North America were examined. The dataset was developed from the literature and consisted of recent species presence/absence (282 species) in each drainage unit; subspecies were not included. Patterns of mussel diversity were examined with hierarchical cluster analysis, based on a pairwise distance matrix between all drainage units.

Results Cluster analysis revealed 17 faunal provinces within four major faunal regions: Mississippian, Atlantic, Eastern Gulf and Pacific. The Mississippian Region dominates the North American fauna with 11 provinces, including five not recognized by previous classifications: Mississippi Embayment, Upper Mississippi, Great Plains, Ohioan and Pontchartrain–Pearl–Pascagoula. Within the Eastern Gulf Region (containing three provinces), the Escambia–Choctawhatchee Province is distinctive from the Apalachicolan Province, under which it was previously subsumed. Patterns of diversity in the Atlantic Region (two provinces) and Pacific Region (one province) were similar to previous classifications.

Main conclusions The classification proposed in this study largely corroborates earlier schemes based on the occurrence of endemic species but identifies additional heterogeneity that reflects unique assemblages of widely distributed species. The study proposes a hierarchical structure that illustrates relationships among these provinces. Although some provinces in the Mississippian Region have high endemism, all Mississippian provinces share a group of widely distributed species. The Atlantic and Eastern Gulf regions have distinctive, endemic faunas suggesting limited past connectivity with the Mississippian Region. The Pacific Region is the most distinct fauna in North America and bears close affinity to the Eurasian mussel fauna.

Keywords

Biogeography, diversity, endemism, faunal regions, freshwater mussels, Margaritiferidae, North America, phylogeography, Unionidae.

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INTRODUCTION

Freshwater bivalves occur world-wide with the exception of Antarctica (Bogan, 2008). The highest diversity of freshwater bivalves is within the order Unionoida; within this group the highest diversity is found in North America, which is home to *c.* 300 taxa (species and subspecies) within the families Unionidae and Margaritiferidae (Graf & Cummings, 2007; Bogan, 2008). Due to the great diversity and imperilled status of the North American fauna, these animals have been the focus of intensive study (e.g. Strayer, 2008), and the distributions of most North American species are now well known. Most unionoid species have a unique life cycle in which larvae (glochidia) require a brief period as parasites on fishes. Many mussel species are host specialists and the fish species required as hosts by specialists vary widely among these species (Barnhart *et al.*, 2008). Because of this host–parasite relationship, distributions of mussels are linked to distributions of their host fishes to varying degrees (Watters, 1992; Haag & Warren, 1998; Vaughn & Taylor, 2000).

Over the past 100 years there have been several attempts to classify North American mussel diversity into biogeographical faunal regions. Early classifications divided the fauna according to the three major drainage realms of North America: the Gulf of Mexico, the Atlantic Ocean and the Pacific Ocean (Table 1); Arctic Ocean river systems have typically not been considered in faunal classifications because they support few or no mussel species. Successive efforts divided the fauna more finely within these realms as better and more complete distributional information became available (Table 1; see Parmalee & Bogan, 1998, for a complete history of biogeographical schemes).

Past faunal classifications were erected and defined based primarily on the presence of endemic species and subjective, intuitive assessments of faunal differences among major river systems. Apart from a lack of objectivity, this approach has the additional shortcoming of failing to recognize potentially distinct assemblages that are not defined by endemic species. Furthermore, most attempts to refine biogeographical schemes have occurred piece-meal as regional specialists subdivided the fauna of a particular area of interest apart from the broader context of continent-wide patterns of diversity (e.g. Clench & Turner, 1956; Neck, 1982). Only a single study (Sepkoski & Rex, 1974) has analysed patterns of mussel species distributions using objective, analytical methods, but this study was limited to river systems flowing into the Atlantic Ocean. Although the presence of endemic species is an important indicator of biogeographically meaningful groups, the subjective methodology or limited geographical scope of previous faunal classifications do not provide a defensible, continent-wide portrayal of patterns of mussel diversity. In this paper I provide a more rigorous and testable classification of mussel diversity within a hierarchical framework that can better inform the biogeographical history of these faunas.

MATERIALS AND METHODS

The dataset

The occurrence of mussel species was compiled for 135 drainage units within 126 river systems or lake watersheds across North America (Table 2). Drainage units were defined using the following criteria. For all river systems except those

Table 1 History of biogeographical classifications for North American freshwater mussels.

Simpson (1900)	van der Schalie & van der Schalie (1950)	Roback *et al.* (1980)	Parmalee & Bogan (1998)	This study
Mississippi	Interior Basin (Mississippi)	Interior Basin	Interior Basin (Mississippian)	Mississippi Embayment
				Upper Mississippi
				Great Plains
				Ohioan
	Cumberlandian	Cumberlandian*	Cumberlandian	Tennessee–Cumberland
	Ozark	Ozarkian*	Ozarkian	Interior Highlands
		Great Lakes–St Lawrence		St Lawrence–Great Lakes
		Central Gulf Coast		Pontchartrain–Pearl–Pascagoula
		Mobile Basin	Mobile Basin	Mobile Basin
		Western Gulf Coast	Sabine	Sabine–Trinity
			Central Texas	Western Gulf
			Rio Grande	
	Apalachicolan (West Floridian)	Apalachicolan	Eastern Gulf Coast (Apalachicolan)	Apalachicolan
				Escambia–Choctawhatchee
Atlantic	Southern Atlantic†	South Atlantic	Southern Atlantic Slope	Southern Atlantic
	Northern Atlantic†	North Atlantic	Northern Atlantic Slope	Northern Atlantic
		Peninsular Florida	Peninsular Florida	Peninsular Florida
Palaearctic	Pacific	Pacific	Pacific	Pacific

*Considered subregions or provinces within the Interior Basin.
†Considered subregions or provinces within the Atlantic Region.

Table 2 Drainage units in North America used to examine patterns of freshwater mussel diversity and faunal affinities. Definitions of drainage units are given for each unit where necessary. Unit numbers correspond to those in Fig. 1. Drainage units without numbers were not included in the cluster analysis because they had two or fewer species. US state or Canadian province abbreviations are given to distinguish rivers with identical names. Information sources for distributional data are given in Appendix S1.

Mississippi River Basin	
	Upper Mississippi River system: (1) Upper Mississippi mainstem (upstream of mouth of Ohio River), (2) Meramec, (3) Illinois (IL), (4) Salt (MO), (5) Kaskaskia, (6) Rock, (7) Wisconsin, (8) Iowa, (9) Minnesota, (10) Chippewa, (11) St Croix (MN, WI)
	Missouri River system: Upper Missouri mainstem (upstream of Great Falls within Rocky Mountains), (12) middle Missouri mainstem (from Great Falls downstream to Niobrara River, within Great Plains physiographic province), (13) lower Missouri mainstem (downstream of Niobrara River, within Central Lowlands physiographic province), (14) Osage, (15) Gasconade, (16) Grand (IA, MO), (17) Kansas, (18) Platte (CO, NE, WY), (19) James (ND, SD), (20) Big Sioux, Yellowstone, Musselshell, Milk, (21) Platte (IA, MO)
	Ohio River system: (22) Ohio River mainstem, (23) Allegheny, (24) Muskingum, (25) Kanawha, (26) Scioto, (27) Kentucky, (28) Green (KY), (29) Licking (KY), (30) Wabash, (31) upper Tennessee (upstream and inclusive of Bear Creek, AL and MS), (32) lower Tennessee (downstream of Bear Creek), (33) upper Cumberland (upstream and inclusive of Red River, KY and TN), (34) lower Cumberland, (downstream of Red River)
	Lower Mississippi River system: (35) lower Mississippi mainstem (downstream of mouth of Ohio River), (36) Hatchie, (37) Big Black, (38) Yazoo, (39) lower St Francis (within Coastal Plain physiographic province), (40) upper St Francis (within Interior Highlands physiographic division), (41) lower White (within Coastal Plain physiographic province), (42) upper White (within Interior Highlands physiographic division), (43) lower Ouachita (within Coastal Plain physiographic province), (44) upper Ouachita (within Interior Highlands physiographic division), (45) Bayou Bartholomew, (46) Tensas, (47) lower Arkansas (within Coastal Plain physiographic province), (48) middle Arkansas (within Interior Highlands physiographic division), (49) upper Arkansas (within Central Lowlands and Great Plains physiographic provinces), (50) Canadian, (51) Neosho, (52) Verdigris, (53) Illinois (AR, OK), (54) upper Red (OK, TX, upstream of Washita River, within Central Lowlands and Great Plains physiographic provinces), (55) lower Red (AR, LA, OK, TX, downstream of Washita River, within Coastal Plain physiographic province), (56) Kiamichi, (57) Little (AR, OK), (58) Atchafalaya
Gulf of Mexico (exclusive of Mississippi River basin)	
	Texas/Louisiana/Mississippi: (59) Rio Grande, (60) Nueces, (61) Guadalupe, (62) Colorado (TX), (63) Brazos, (64) Trinity, (65) Neches, (66) Sabine, (67) Calcasieu, (68) Pontchartrain, (69) Pearl, (70) Pascagoula
	Mobile Basin: (71) Alabama, (72) Tombigbee
	Alabama/Georgia/Florida: (73) Escambia, (74) Yellow, (75) Choctawhatchee, (76) Apalachicola, (77) Ochlockonee, (78) Suwannee, (79) Withlacoochee, (80) Hillsborough, (81) Peace (FL)/Myakka, Caloosahatchee, (82) Kissimmee/Okeechobee
Atlantic Ocean	
	(83) St Johns (FL), (84) Altamaha, (85) Ogeechee, (86) Savannah, (87) Waccamaw, (88) Santee, (89) Pee Dee, (90) Cape Fear, (91) Neuse, (92) Tar, (93) Roanoke, (94) Chowan, (95) James (VA), (96) Rappahannock, (97) Potomac, (98) Susquehanna, (99) Delaware, (100) Hudson, (101) Connecticut, (102) Merrimack, (103) Androscoggin, (104) Kennebec, (105) Penobscot, (106) St Croix (ME, NB), (107) St John (ME, NB), (108) Charles, (109) Petitcodiac
Pacific and Arctic oceans	
	(110) Sacramento, (111) Eel, (112) Klamath, (113) Rouge, (114) Umpqua, (115) Columbia, (116) Fraser, Southeast Alaska rivers, Yukon, McKenzie, (117) Great Basin, Colorado (AZ, CA, CO, WY)
Hudson Bay	
	(118) Red (MB, MN, ND)/Assiniboine, (119) Saskatchewan, (120) Nelson/Churchill
Great Lakes	
	(121) St Lawrence/Ottawa, (122) Lake Ontario, (123) Lake Erie/St Clair, (124) Lake Huron, (125) Lake Michigan, (126) Lake Superior

within the Mississippi, Mobile and Great Lakes basins, and the Great Basin, units included all portions of a system emptying into the sea through a common outlet. For example, the Apalachicola unit included the Chattahoochee, Flint and Chipola rivers as well as the main stem Apalachicola River and all other tributaries in the system. Within the Mobile River basin, the Tombigbee and Alabama river systems were considered to be separate units because of their large size and because they are confluent only a short distance above salt water. For the Great Lakes, each major lake and its respective tributaries were considered collectively as an individual unit. For example, the Lake Michigan unit included the lake itself as well as tributaries to the lake. Lake St Clair and its tributaries were included in the Lake Erie unit (Erie/St Clair). The Great Basin of the western United States includes a series of endorheic river systems; these systems were included collectively in a single Great Basin unit.

Within the Mississippi River basin, units were defined as river systems that flow directly into the Mississippi, Missouri or Ohio rivers, and the main stems of each of these three rivers were considered to be separate units. Some river units in the Mississippi River basin were subdivided to account for major differences in physical characteristics of river segments as they flow through different physiographic regions as described in Benke & Cushing (2005) (see Table 2). The Mississippi River main stem was divided into an upper and lower unit at the mouth of the Ohio River, which approximates the point at which the river flows onto the Gulf Coastal Plain physiographic province. Similarly, several tributaries of the Mississippi River were divided into upper and lower units at the point where they flowed from uplands onto the Gulf Coastal Plain (Ouachita, Red, White and St Francis rivers). The Arkansas River system was divided into three units: lower (within the Coastal Plain), middle (within the Interior

Highlands physiographic division) and upper (within the Central Lowlands and Great Plains physiographic provinces). Within the Interior Highlands physiographic division of the south-central United States, several smaller rivers were considered to be separate units (e.g. Neosho, Verdigris, Kiamichi, Little) because they are essentially upland streams that flow into larger streams with radically different physical characteristics (Arkansas and Red rivers). The upper and lower sections of both the Cumberland and Tennessee rivers have long been considered to contain two distinct faunal assemblages (Ortmann, 1924, 1925); to test this idea, these rivers were divided into two units corresponding to previously defined boundaries between their upper and lower faunas (see Table 2). The upper and lower sections of these rivers also differ physically because the lower sections assume lowland characteristics as they approach the Coastal Plain (Burr & Warren, 1986; Etnier & Starnes, 1993). The Missouri River main stem was divided into three units: upper (above Great Falls within the Rocky Mountains), middle (from Great Falls to the Niobrara River, within the Great Plains physiographic province) and lower (below Niobrara River, within the Central Lowlands physiographic province).

Species presence/absence in each unit was determined based on historical or recent occurrence. Species occurrence was obtained from a wide variety of sources, including published primary literature, state and regional mussel guides, unpublished technical reports and museum collection records (see Appendix S1 in Supporting Information). Archaeological records of species occurrence were not included in the dataset because I was primarily interested in recent patterns of species distribution, and because archaeological data are unavailable for many areas. For some rivers, the original fauna prior to major 20th century stream degradation is poorly known (e.g. Des Moines and Monongahela rivers), and these rivers were omitted from the dataset.

Species recognition and taxonomy was based on Turgeon *et al.* (1998) but incorporated recent taxonomic changes reported in Williams *et al.* (2008) and J. D. Williams *et al.* (Florida Museum of Natural History, Gainseville, FL, unpublished data). Deviations from standard nomenclature were made in the following cases. First, I did not include subspecies or undescribed species because of uncertainties about the taxonomic validity and distribution of many of these taxa. Second, two species (*Anodonta beringiana* and *Anodonta dejecta*) were excluded from the analysis because they occurred only in drainage units that had two or fewer species (see 'Data analysis and recognition of faunal groupings'). Third, several currently recognized species that are morphologically similar were combined into single taxa because past confusion about their identification or taxonomic validity makes their ranges difficult to ascertain from available information. These species were *Lampsilis satura* (combined with *Lampsilis cardium*) and *Lampsilis hydiana* (combined with *Lampsilis siliquoidea*) (see Vaughn *et al.*, 1996), *Pyganodon lacustris* (combined with *Pyganodon grandis*) (see Strayer & Jirka, 1997), *Quadrula mortoni* (combined with *Quadrula pustulosa*) and *Quadrula nobilis* (combined with *Quadrula quadrula*) (see Howells *et al.*, 1996) and all five recognized species of *Uniomerus*, which were treated collectively as *Uniomerus* spp. (see Williams *et al.*, 2008). The resulting dataset included a total of 282 species.

Data analysis and recognition of faunal groupings

Hierarchical cluster analysis, based on a pairwise distance matrix between all drainage units, was used to examine patterns of mussel diversity. Units were clustered using two different methods – Euclidean distance with Ward's linkage method and Sørensen distance with unweighted pair group method with arithmetic mean (UPGMA) linkage – and dendrograms were constructed to depict results (McCune & Grace, 2002). For cluster analysis, units with two or fewer species were deleted from the dataset because the inclusion of sparse units can give spurious or nonsensical results. The dataset used in cluster analysis contained 126 drainage units (Table 2). All clustering analyses were conducted with PC-ORD (McCune & Mefford, 2006).

Attempts to use an objective method for recognizing natural groupings (indicator species analysis, Dufrêne & Legendre, 1997) resulted in a proliferation of groups that made little sense biogeographically. This was probably due to the size of the dataset (126 drainage units × 282 species) and the presence/absence nature of the data. Therefore, to identify important groupings, dendrograms were pruned at a distance measure that minimized recognition of potentially spurious or biogeographically meaningless entities yet reflected strong, consistent faunal differences among rivers (McCune & Grace, 2002). Clustering based on both Euclidean and Sørensen distance measures supported recognition of 17 faunal provinces that were made up of nearly identical groups of drainage units (see Results). Based on these results, a composite fauna was produced for each province (composite of species presence/absence in all drainage units within each province) and the resulting matrix (17 provinces × 282 species) was clustered according to the methods described above. This analysis provided a clearer portrayal of relationships between provinces as well as higher-level faunal groupings.

Terminology

A hierarchical scheme was used to portray patterns of mussel diversity in which 'regions' describe large-scale groupings and 'provinces' identify finer-scale subdivisions within regions (e.g. Darlington, 1957; Procheş, 2005).

RESULTS AND DISCUSSION

Results of cluster analysis

By pruning the dendrogram at a distance measure of *c.* 686.7 (objective distance function; see McCune & Grace, 2002), Euclidean distance identified 18 faunal groups (Fig. 1, but see below). This pruning point supports the distinctiveness of

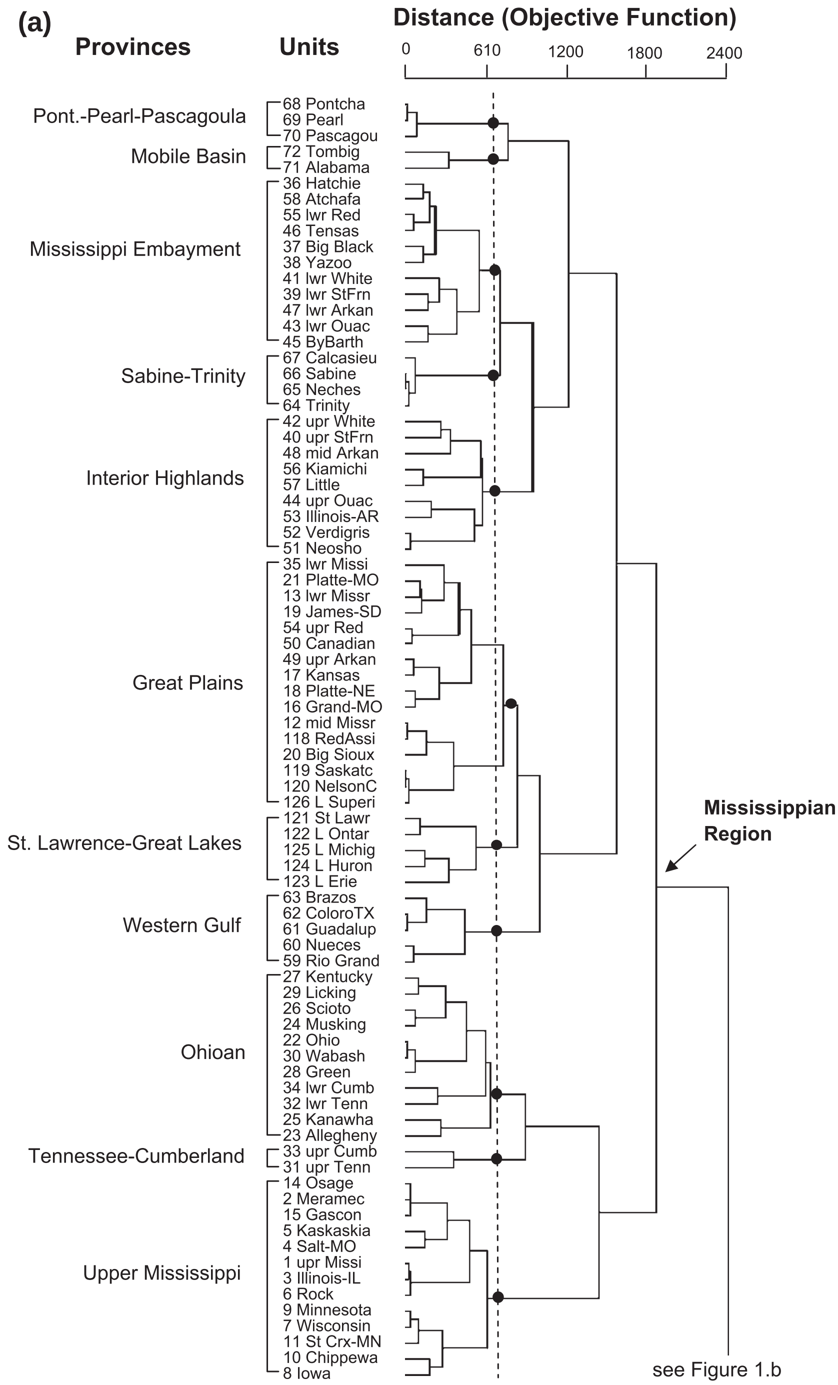

Figure 1 Dendrogram (Euclidean distance with Ward's linkage method) depicting relationships among the mussel faunas of 126 drainage units in North America (percentage chaining = 1.22). Numbers for each drainage unit are cross-referenced in Table 2. The dashed vertical line at a distance value of 686.7 indicates the pruning point used to recognize all faunal provinces except the Great Plains province; the two groups within the Great Plains province were considered as a single faunal province (see text). The dendrogram is split between panels (a) and (b).

faunal provinces that have been recognized previously based on the presence of endemic species (e.g. Tennessee–Cumberland, Interior Highlands, Sabine–Trinity, Southern and Northern Atlantic, Peninsular Florida, Pacific; Table 1) and identified other previously unrecognized groups that nevertheless have distinctive assemblages (e.g. Mississippi Embayment, Ohioan, Great Plains, Escambia–Choctawhatchee, Pontchartrain–Pearl–Pascagoula; see subsequent discussion of faunal provinces). At this pruning point, only a single group was identified that has little or no biogeographical importance. Rivers of the Great Plains were split into two groups that overlap geographically, both containing portions of the Missouri River system

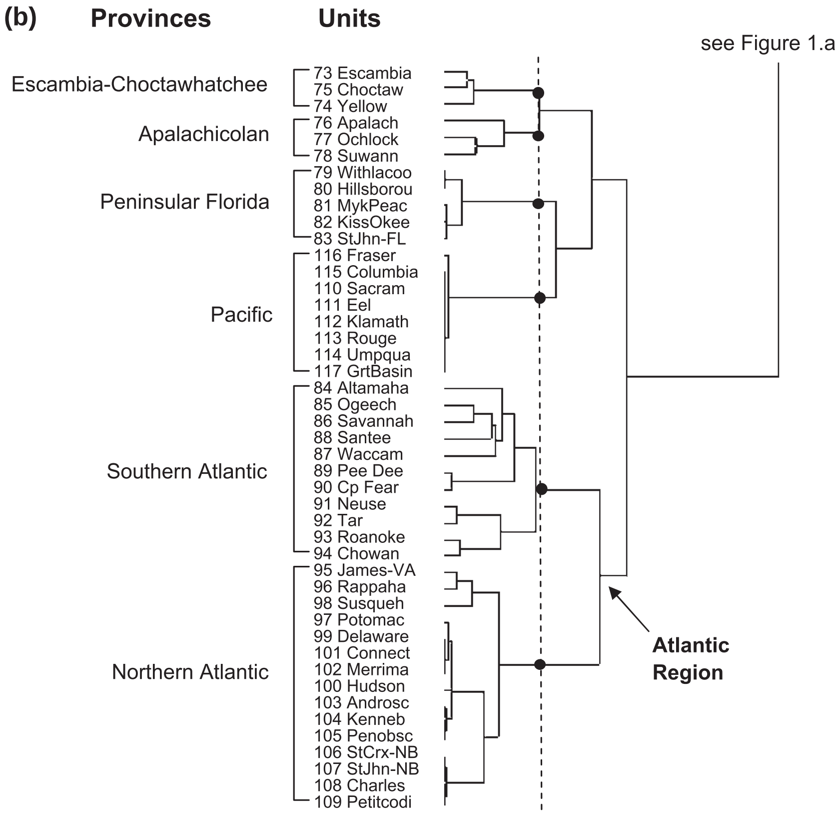

Figure 1 Continued

(Fig. 1). Streams in the Great Plains are faunistically depauperate and heterogeneous due to variable and stressful physical conditions (see subsequent discussion of faunal provinces). The division of these rivers into two groups is therefore likely to be an artefact of the clustering algorithm as it attempted to group drainage units with depauperate and variable faunas; for this reason, I considered rivers within these two groups to represent a single faunal group – the Great Plains Province. Combining Great Plains streams into a single group resulted in the recognition of 17 faunal provinces in North America (Table 3, Fig. 2).

Clustering by both Euclidean and Sørensen distance placed the lower Mississippi River and Lake Superior with the Great Plains Province (Fig. 1), but these results probably reflect weaknesses of the clustering algorithm in categorizing depauperate faunas composed of widespread species. Like streams in the Great Plains, the lower Mississippi River is highly dynamic and unstable, and consequently supports relatively few mussel species (van der Schalie & van der Schalie, 1950). However, the presence of characteristic Mississippi Embayment species, such as *Anodonta suborbiculata*, *Potamilus capax* and *Potamilus purpuratus* (Cooper, 1984; Cicerello *et al.*, 1991; Jones *et al.*, 2005), indicate that the lower Mississippi River is most simply viewed as having a depauperate subset of the Mississippi Embayment Province fauna. For similar reasons, Lake Superior can be considered to belong within the St Lawrence–Great Lakes Province. The depauperate fauna of Lake Superior (eight species) has a biogeographical history similar to the other Great Lakes, having colonized via interlake basin dispersal from post-Pleistocene connections with the Mississippi River basin and the Atlantic coast (Graf, 1997), and is distinguished by the presence of *Elliptio complanata*, a species present throughout the Great Lakes but absent in the Mississippi River basin.

Clustering of drainage units based on Sørensen distance identified faunal groupings (not illustrated) that were nearly identical to those identified by Euclidean distance. Although the composition of terminal clusters was similar between the two methods, the dendrogram based on Sørensen distance could not be pruned at a single distance value that minimized both the recognition of groups with no biogeographical meaning and the aggregation of groups with highly distinctive faunas. For example, pruning the dendrogram at a distance value that preserved the identity of the Tennessee–Cumberland Province, one of the most distinctive faunal assemblages in North America (e.g. Ortmann, 1925; Parmalee & Bogan, 1998), also resulted in the separation of depauperate Great Plains rivers into six faunal groups. The only difference in the composition of groups identified by the two methods was that Sørensen distance separated rivers in the Interior Highlands physiographic division into three groups, corresponding to the Ozark (one group) and Ouachita uplands (two groups), respectively, and placed these groups in different areas of the dendrogram (Ozark rivers clustered nearest to the upper Mississippi River Province and both Ouachita groups clustered nearest to the Mississippi Embayment). Euclidean distance clustered all Interior Highlands rivers into a single group, and

Table 3 Freshwater mussel faunal regions and provinces of North America. Provinces were identified by cluster analysis of 126 drainage units (see Table 2) but, in some cases, boundaries of provinces were refined using cited distributional information for rivers not included in cluster analysis (e.g. Waccasassa and St Mary's rivers in Florida Peninsula Province, see below). Total richness and number of endemic species in each province was determined from the distributional dataset (see text).

	Total richness	No. endemic species	Definition
1.0 Mississippian Region			
1.1 Mississippi Embayment Province	59	1 (2%)	Lower Mississippi River system downstream of mouth of Ohio River; Atchafalaya Basin; lower portions of Arkansas, Ouachita, Red, St Francis, White river systems within Coastal Plain physiographic province
1.2 Upper Mississippi Province	55	1 (2%)	Upper Mississippi River system upstream of mouth of Ohio River; Osage, Gasconade river systems, excl. remainder of Missouri River system
1.3 Ohioan Province	78	3 (4%)	Entire Ohio River system excl. *c.* upper two-thirds of Cumberland, Tennessee river systems (see below)
1.4 Tennessee–Cumberland Province	110	31 (28%)	Tennessee River system upstream of and incl. Bear Creek system and incl. middle and upper Duck and Buffalo river systems; Cumberland River system upstream of and incl. Red River system (see text)
1.5 Interior Highlands Province	63	9 (14%)	Upper White, upper St Francis river systems within Ozark Plateaus physiographic province; upper Ouachita River system within Ouachita physiographic province; Verdigris, Neosho river systems; middle Arkansas River system within Ouachita and Ozark Plateaus physiographic provinces; Kiamichi, Little river systems
1.6 Great Plains Province	37	0	Upper Red and upper Arkansas River systems within Central Lowlands and Great Plains physiographic provinces; Missouri River system excl. Osage and Gasconade river systems; Nelson-Churchill Basin
1.7 St Lawrence–Great Lakes Province	47	0	Great Lakes, Lake St Clair and their watersheds; St Lawrence River system
1.8 Western Gulf Province	31	11 (35%)	Rivers flowing into the Gulf of Mexico from Brazos River south to the Rio Grande
1.9 Sabine–Trinity Province	34	4 (12%)	Rivers of the central Gulf Coast from Trinity to Calcasieu rivers
1.10 Pontchartrain–Pearl–Pascagoula Province	38	2 (5%)	Pearl and Pascagoula river systems; rivers flowing into lakes Pontchartrain and Maurepas
1.11 Mobile Basin Province	72	32 (44%)	Rivers flowing into Mobile Bay in the Gulf of Mexico
2.0 Eastern Gulf Region			
2.1 Escambia–Choctawhatchee Province	33	11 (33%)	Escambia, Yellow, Choctawhatchee river systems
2.2 Apalachicolan Province	37	14 (38%)	Apalachicola, Ochlockonee, Suwannee river systems
2.3 Peninsular Florida Province	14	5 (36%)	Waccasassa River on Gulf Coast to St Mary's River on Atlantic Coast (see Johnson, 1970; Butler, 1989)
3.0 Atlantic Region			
3.1 Southern Atlantic Province	46	27 (59%)	Satilla River north to James River, VA (see text)
3.2 Northern Atlantic Province	20	1 (5%)	York River system, VA (see text) to Newfoundland
4.0 Pacific Region			
4.1 Pacific Province	6	4 (67%)	Rivers of North America flowing into the Pacific Ocean (incl. Gulf of California) and Bering and Beaufort seas

relationships within this group did not support a strong split between an Ozark and Ouachita fauna (Fig. 1).

Sørensen distance clustered the composite faunas of each of the 17 faunal provinces identified above into four major faunal regions: Mississippian, Eastern Gulf, Atlantic and Pacific (Fig. 3). Clustering based on Euclidean distance showed a similar regional scheme supporting the inclusiveness of the Mississippian Region and the distinctiveness of the Atlantic Region (Fig. 1). However, it also identified a biogeographically nonsensical sister-group relationship between the Pacific and Peninsular Florida provinces (Fig. 1); these provinces both have low diversity and high endemism but share no species.

Faunal regions

The four faunal regions identified by this analysis depict broad-scale patterns of mussel diversity in North America. The Pacific Region has the most distinctive fauna (Fig. 3), sharing only a single species with other regions in North America. Phylogenetic relationships of species in the Pacific Region suggest that this fauna has close biogeographical affinities to Eurasia and has followed an evolutionary trajectory largely independent from the remainder of the North American mussel fauna; this affinity was apparently noted by Simpson (1900) who referred to this province as the 'Palearctic Region'

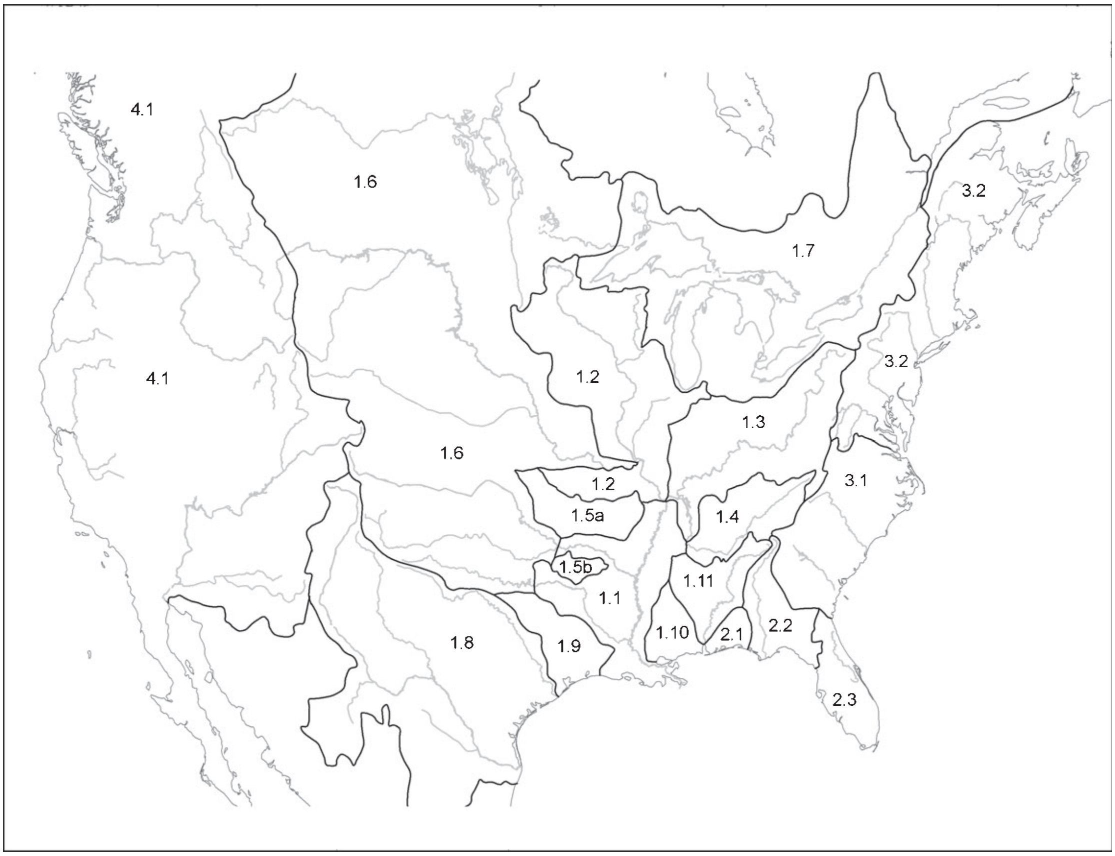

Figure 2 Freshwater mussel faunal regions and provinces of North America. Regions are composed of all provinces with the same integer as follows: 1, Mississippian; 2, Eastern Gulf; 3, Atlantic; 4, Pacific. Provinces within the same region have the same integer but different decimal numbers and are identified as follows: 1.1, Mississippi Embayment; 1.2, Upper Mississippi; 1.3, Ohioan; 1.4, Tennessee–Cumberland; 1.5, Interior Highlands; 1.6, Great Plains; 1.7, St Lawrence–Great Lakes; 1.8, Western Gulf; 1.9, Sabine–Trinity; 1.10, Pontchartrain–Pearl–Pascagoula; 1.11, Mobile Basin; 2.1, Escambia–Choctawhatchee; 2.2, Apalachicolan; 2.3, Peninsular Florida; 3.1, Southern Atlantic; 3.2, Northern Atlantic; 4.1, Pacific (see Table 3 for a detailed description of province boundaries). For the Interior Highlands Province (1.5), letters represent the two disjunct units of this province within the Ozark (a) and Ouachita (b) uplands (see text); this notation is for reference purposes only and does not reflect clustering results (see Fig. 1).

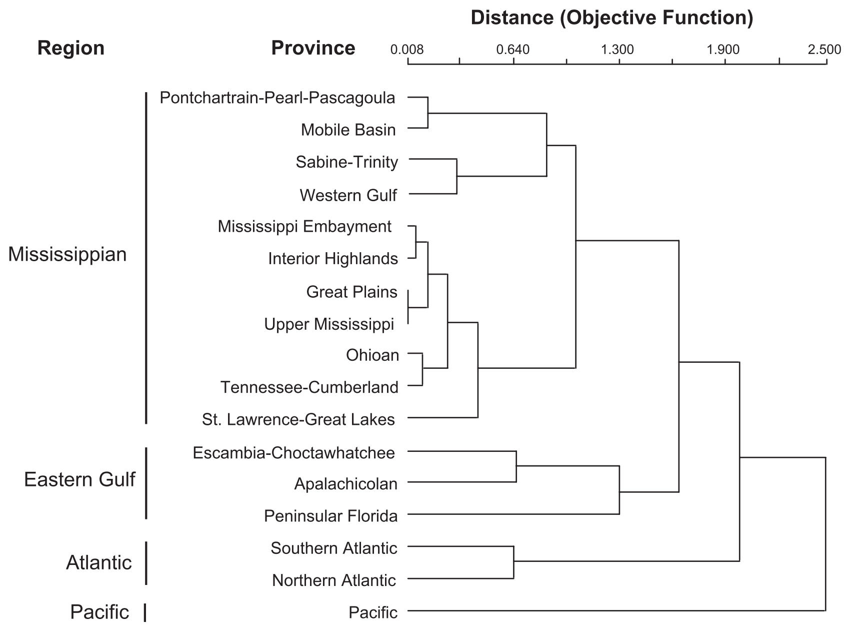

Figure 3 Dendrogram (Sørensen distance with unweighted pair group method with arithmetic mean (UPGMA) linkage) depicting relationships among freshwater mussel faunal regions and provinces of North America (percentage chaining = 31.71).

(Table 1). The Pacific Region species *Gonidea angulata* and *Margaritifera falcata* appear more closely related to Eurasian species than to any North American species (Smith, 2001; Campbell *et al.*, 2005). Similarly, *Anodonta beringiana* also occurs in Kamchatka in eastern Asia (Nedeau *et al.*, 2009) and is more closely related to the Asian species *Anodonta woodiana* than to North American *Anodonta* (Chong *et al.*, 2008). The relationships of other Pacific Region *Anodonta* remain unclear, but their affinity to the Eurasian species *Pseudanodonta complanata* suggests an evolutionary connection to Eurasia for these species as well (Chong *et al.*, 2008). Past exchange between the Pacific Region and other faunal regions in North America appears limited to Pleistocene capture of headwater streams of the Columbia River system by the upper Missouri River system, which allowed colonization of the latter system by *M. falcata* (Gangloff & Gustafson, 2000). However, the distribution of this species within the Mississippi River basin has apparently been limited by the physical barrier of Great Falls on the Missouri River and the absence of habitat for its fish hosts (trout) in the Missouri River system beyond the Rocky Mountains.

The other three North American faunal regions have shared mussel species, which suggests a shared biogeographical history to varying extents. The Atlantic Region has a highly distinctive fauna (Figs 1 & 3), composed of about 52 species (37 endemic), but shares few species with the Mississippian (10 species) and Eastern Gulf (7 species) Regions, suggesting that it, like the Pacific Region, has followed a largely independent evolutionary trajectory. However, the fauna of the Atlantic Region is clearly of North American origin (e.g. King *et al.*, 1999; Campbell *et al.*, 2005) and includes many genera endemic to North America (e.g. *Alasmidonta*, *Elliptio*, *Lampsilis*, *Lasmigona*, *Villosa*). The only Atlantic species of probable Eurasian affinity is the Holarctic species *Margaritifera margaritifera*.

The mussel fauna of North America is dominated by the Mississippian Region, which includes 11 of the 17 faunal provinces (Table 3) and encompasses the entire Mississippi River basin, the St Lawrence–Great Lakes system, the Mobile River basin, the Lake Pontchartrain, Pearl and Pascagoula river systems and all Gulf of Mexico river systems west of the Mississippi River (Figs 2 & 3). The region contains about 198 species, or two-thirds of the North American fauna, of which 147 (74%) are endemic to the region. The major faunal split in the Mississippian Region is between two groups: (1) the Mississippi River basin plus the Great Lakes, and (2) all other Gulf of Mexico river systems from and including the Mobile River basin west (Fig. 3). The Mississippi River basin alone contains 133 species, many of which are widespread in all six provinces in the basin. The faunas of other Mississippian provinces bear strong affinity to the Mississippi River basin fauna. Apart from endemic species that characterize each province, the St Lawrence–Great Lakes, Mobile Basin, Pontchartrain–Pearl–Pascagoula, Sabine–Trinity and Western Gulf Provinces are dominated by species that are shared with the Mississippi River basin, supporting the inclusiveness of the Mississippian Region.

The Eastern Gulf Region includes three provinces that encompass river systems of the Gulf of Mexico from the Escambia River east, and river systems of the Florida peninsula, north to the St Mary's River on the Atlantic coast (Table 3, Figs 2 & 3). The Eastern Gulf fauna is distinctive, including a large number of endemic species (34 of a total of 58 species), but has affinities with the Mississippian Region (Fig. 3) with which it shares 17 species, including several genera that are absent in the Atlantic Region (*Amblema*, *Anodontoides*, *Glebula*, *Hamiota*, *Medionidus*, *Megalonaias*, *Pleurobema*, and *Quadrula*; note that '*Pleurobema*' *collina* of the Atlantic Coast is more closely related to *Elliptio* than to *Pleurobema*, Campbell *et al.*, 2005). Despite these similarities, there is an abrupt and profound faunal shift between the Mobile Basin Province in the Mississippian Region and the adjacent Escambia–Choctawhatchee River Province and other faunal provinces of the Eastern Gulf Region. The Mobile Basin Province and the Eastern Gulf Region share only a single genus (*Hamiota*) that is not also present elsewhere in the Mississippian Region. In contrast, a large number of genera are shared by the Mobile Basin and Mississippi River basin but are absent in the Eastern Gulf Region [*Arcidens*, *Ellipsaria*, *Epioblasma*, *Leptodea*, *Ligumia*, *Obliquaria*, *Plectomerus*, *Potamilus*, '*Tritogonia*' (within *Quadrula*) and *Truncilla*].

Faunal provinces

The 17 faunal provinces identified in this analysis largely corroborate previous biogeographical classifications (Table 1) but refine these ideas primarily by showing important patterns of additional heterogeneity within previously recognized groups. Most notably, the 'Interior Basin' was used by previous schemes as a catch-all group for several unrecognized yet distinctive faunas, including those of the Ohioan, Mississippi Embayment, Upper Mississippi, Great Plains, St Lawrence–Great Lakes and Pontchartrain–Pearl–Pascagoula provinces (Table 1). The distinctive and diverse faunas of the Mississippi Embayment, and particularly the Ohioan Province, were noted earlier (Ortmann, 1925; Johnson, 1980; Parmalee & Bogan, 1998), even though these provinces were not recognized in previous classification schemes. The St Lawrence–Great Lakes and Pontchartrain–Pearl–Pascagoula (as 'Central Gulf Coast') provinces were recognized by Roback *et al.* (1980) but subsumed within the 'Interior Basin' by Parmalee & Bogan (1998), even though the Pontchartrain–Pearl–Pascagoula Province bears closest affinity to the Mobile Basin Province (Figs 1 & 3). The Upper Mississippi and Great Plains provinces have not been recognized previously.

The Escambia–Choctawhatchee Province was previously subsumed within the Apalachicolan Province (Table 1), conflating the highly distinctive nature of these two faunas. However, Butler (1989) noted a major faunal break between the Choctawhatchee and Apalachicola rivers. My clustering results confirm this observation, showing a deep split between these two provinces at a level comparable to that which characterizes other, previously recognized faunal provinces (e.g. Mobile Basin, Peninsular Florida, Sabine–Trinity; Fig. 1). The failure of previous schemes to recognize the Escambia–Choctawhatchee Province is puzzling given that it contains a higher percentage of endemic species (11 species, 33%) than several other previously recognized provinces (e.g. Interior Highlands, Northern Atlantic, Sabine–Trinity, Tennessee–Cumberland; Table 3), and out of 54 total species in the Escambia–Choctawhatchee and Apalachicolan Provinces combined, only 16 species are shared by both provinces.

Additional patterns of faunal heterogeneity

Ohioan and Tennessee–Cumberland provinces

The upland faunas of the Ohioan and Tennessee–Cumberland provinces contain the highest mussel richness and endemism in North America (Table 3). Including species shared exclusively by both provinces, these faunas collectively include over 44 endemic species and at least five endemic genera. Based on its high endemism (31 species, 4 genera) the distinctiveness of the Tennessee–Cumberland Province has been recognized for many years (e.g. Ortmann, 1924; Parmalee & Bogan, 1998), and the province supports a similarly rich and distinctive fish fauna (Starnes & Etnier, 1986).

The distribution of endemic mussel species is curiously truncated in both the Tennessee and Cumberland river systems, abruptly disappearing in about the lower third of these rivers (Ortmann, 1924, 1925). Furthermore, a tributary of the lower Tennessee River, the Duck River, shows a similar pattern, having Tennessee–Cumberland Province endemic species in its upper and middle portion but few or none in the lower section (Ortmann, 1924). Clustering results support the grouping of the lower Cumberland and lower Tennessee rivers with the Ohioan Province (Fig. 1). Although my dataset did not consider the Duck River apart from the Tennessee River system, the lower section of the Duck River is included in the Ohioan Province (see Fig. 2) based on the absence of most endemic species that characterize the Tennessee–Cumberland Province (e.g. Ortmann, 1924; Schilling & Williams, 2002).

The absence of endemic species in the lower part of the Cumberland and Tennessee river systems, as well as in the lower Duck River system, is unexplained but their disappearance coincides roughly with the point at which these rivers enter channels with lowland characteristics as they approach the Coastal Plain (Burr & Warren, 1986; Etnier & Starnes, 1993). Because endemic species of the Tennessee–Cumberland Province typically inhabit upland streams, their present-day distribution may be truncated by an absence of this habitat in the lower portions of these rivers. However, archaeological evidence suggests that endemic species in the Cumberland and Tennessee rivers occurred further downstream, nearly to their mouths, within the last 5000 years (Casey, 1987; Parmalee & Bogan, 1998). In recent times, the mussel fauna of the lower section of both streams is similar and essentially identical to large rivers in the lower portion of the Ohioan Province.

Dispersal in the upper Mississippi River basin and Great Lakes

The upper Mississippi, Great Plains and St Lawrence–Great Lakes provinces have not been recognized previously because these provinces have few or no endemic species that were the primary indicator of faunal groups in earlier classifications. The boundaries of the upper Mississippi Province correspond closely with the maximum extent of Pleistocene glaciation, an event that was instrumental in shaping the fish fauna in this area (Burr & Page, 1986). The upper Mississippi Province clustered into two major groups (Fig. 1) corresponding to rivers in the southern portion of the province with a more diverse fauna (average richness 43 species) and a less diverse group of northern rivers (average richness 37 species). In addition to being closer to sources of recolonization, southern rivers were either not glaciated in the Pleistocene (e.g. Osage, Meramec, Gasconade) or were covered by earlier glacial advances (Kansan, Illinoian) but not by the most recent Wisconsin advance (e.g. Illinois and Kaskaskia rivers) (Burr & Page, 1986; Delong, 2005). In contrast, the fauna of northern rivers in the province is composed largely of species that have colonized these rivers more recently following glaciation. This post-glacial dispersal hypothesis is supported by patterns of genetic variation in both mussels (Burdick & White, 2007) and fishes (Berendzen *et al.*, 2003; Near *et al.*, 2003).

Similar to the upper Mississippi Province, the Great Plains and St Lawrence–Great Lakes provinces are characterized not by endemic species but by assemblages that are unique subsets of larger faunas. The fauna of the northern portion of the Great Plains Province is entirely post-Pleistocene in origin and is composed of a depauperate subset of the Mississippi River basin fauna. Similarly, streams which now flow into Hudson Bay (e.g. Red-Assiniboine) were colonized from the Mississippi River basin via now defunct post-Pleistocene connections between those watersheds (Cvancara, 1970; Graf, 1997). Throughout the Great Plains Province, mussel communities are further limited by arid conditions and hydrological variability that result in highly unstable stream habitats (Hoke, 2005; Matthews *et al.*, 2005), and the fauna is characterized by short-lived or fast-growing species that can adapt to these challenges (e.g. *Anodontoides ferussacianus*, *Lampsilis* spp., *Lasmigona complanata*, *Leptodea fragilis*, *Potamilus* spp., *Pyganodon grandis*, *Uniomerus* sp., *Utterbackia imbecillis*). The fauna of the Great Lakes is a heterogeneous admixture of species from the upper Mississippi, Ohioan and Northern Atlantic provinces, a result of colonization from these provinces following Pleistocene glaciation (van der Schalie, 1963; Clarke & Stansbery, 1988; Graf, 1997). However, the low genetic diversity of many mussel populations in the Great Lakes suggests a limited number of dispersal events

(Krebs *et al.*, 2003; Burdick & White, 2007; Elderkin *et al.*, 2007).

Interior Highlands

The Interior Highlands Province encompasses two geographically discontinuous upland areas, corresponding to streams in the Ozark Plateaus and Ouachita physiographic provinces, respectively (Fig. 2). The Interior Highlands Province has long been recognized based on the presence of endemic species (van der Schalie & van der Schalie, 1950), but the fauna is further characterized by the presence of upland species that are absent in the adjacent Mississippi Embayment Province. The Interior Highlands Province was traditionally referred to as the 'Ozark' or 'Ozarkian' Province (Table 1), but this terminology fails to recognize the unique fauna present in streams in the Ouachita uplands as well. These two upland areas are the remnants of an ancient mountain range that may have been continuous with the Appalachians until they were isolated during the Pleistocene by rises in sea level and subsequent deposition of sediments within the lower Mississippi River valley, leaving relict populations of upland species in the Interior Highlands (Robison, 1986; Mayden, 1988). At about the same time, the Ozark and Ouachita uplands were isolated from each other by development of the intervening lowlands of the Arkansas River valley (Robison, 1986).

The isolation of the Interior Highlands fauna in these remnant upland areas explains the discontinuous distribution of that fauna, a pattern that is also seen in the distribution of many upland fish species (Robison & Buchanan, 1988; Strange & Burr, 1997). All rivers of the Interior Highlands Province flow ultimately onto the Coastal Plain where they assume lowland characteristics typical of the Mississippi Embayment Province, but the boundaries between these two provinces are somewhat fuzzy. The lower sections of the White, St Francis and Ouachita Rivers within the Coastal Plain (and Bayou Bartholomew, a tributary of the lower Ouachita) have typical lowland faunas and cluster with the Mississippi Embayment Province (Fig. 1). However, these rivers formed a distinct cluster within the Mississippi Embayment probably due to the presence of several characteristic Interior Highlands species that transcend to varying extents the upland/lowland boundary (e.g. *Cyprogenia aberti*, *Ptychobranchus occidentalis*). Similarly, some typically lowland species transcend this boundary, also occurring in upland streams in the Interior Highlands Province (e.g. *Ligumia subrostrata*, *Potamilus purpuratus*, *Plectomerus dombeyanus*). These shared faunal elements are reflected in the close relationship between the Interior Highlands and Mississippi Embayment faunas (Figs 1 & 3).

Rio Grande

Based on the presence of endemic species, the Western Gulf Province has been considered previously to be composed of two faunal groups, the 'Rio Grande' and 'Central Texas' provinces (Table 1; Neck, 1982). The Rio Grande and adjacent Nueces River formed a separate cluster within the Western Gulf Province (Fig. 1) and these rivers contain endemic species not found elsewhere in the province. However, the pruning point I used to identify faunal provinces does not support recognition of these rivers as a separate province. The Western Gulf Province, and especially the Rio Grande system, represents a transitional zone between the Mississippian Region mussel fauna of North America and the fauna of northern Mexico and Mesoamerica. Several species in the Rio Grande system also occur in Mexico, but their Mexican distribution is poorly known (e.g. Strenth *et al.*, 2004). Further consideration of the biogeographical affinities of the Rio Grande fauna will require better phylogenetic and distributional information on the mussel species of northern Mexico and Mesoamerica.

Unresolved issues in the Atlantic Region

The Atlantic Region presents the most difficult challenges in understanding biogeographical patterns of mussel diversity in North America. The Northern Atlantic Province has a relatively homogeneous, low-diversity fauna. In contrast, rivers in the Southern Atlantic Province show great faunal heterogeneity, and the province has the highest percentage of endemic species of any province in eastern North America (Table 3). Unlike other provinces that are characterized by widespread endemic species, endemic species in the Southern Atlantic Province appear to be restricted to only one or a few river systems and none are characteristic of the province as a whole. However, the phylogenetic relationships of most species are poorly understood and endemism is likely to be underestimated. Although Sepkoski & Rex (1974) postulated that glochidia could disperse on euryhaline fishes among coastal rivers, based on genetic evidence King *et al.* (1999) concluded that many conspecific populations distributed among isolated Atlantic coast rivers are potentially evolutionarily distinct units. The degree of potential cryptic diversity is exemplified by the bewildering diversity of the genus *Elliptio*, which dominates mussel communities in the Southern Atlantic Province. Within the several recognized species groups of *Elliptio*, each river system often has a highly distinctive form, or several forms (Bogan, 2002; Savidge, 2006; Watters, 2008), but at this time no workable consensus exists for estimates of species diversity within Atlantic *Elliptio*.

The boundary between the Southern and Northern Atlantic Provinces has been placed traditionally in the vicinity of Chesapeake Bay. For fishes, the boundary is considered to be between Albemarle Sound (Chowan–Roanoke river systems) and Chesapeake Bay (James River) (Jenkins & Burkhead, 1994). For mussels, Johnson (1970) placed the boundary between the James (Southern) and York (Northern) river systems (both flowing into Chesapeake Bay). The existence of a biogeographical boundary in this region is supported by DNA sequence divergence between populations of *Lasmigona subviridis* in the Rappahannock and the James river systems (King *et al.*, 1999). My clustering results supported the boundary proposed for fishes by Jenkins & Burkhead (1994), placing the James River within the Northern Atlantic Province (Fig. 1). However, the poor understanding of phylogenetic relationships of mussel species in the Atlantic Region, especially within the genus *Elliptio*, precludes precise demarcation of the boundary between the Southern Atlantic Province and the Northern Atlantic Province at this time. For this discussion, I have followed the boundaries proposed by Johnson (1970) and King *et al.* (1999) (Table 3).

The apparent faunal heterogeneity among rivers suggests that the Southern Atlantic Province may be composed of multiple, distinct faunal groups. A previous clustering analysis of Atlantic coast rivers recognized a Middle Atlantic Province, which extended from the Susquehanna to the Tar river systems (Sepkoski & Rex, 1974). Similarly, my clustering results showed a deep split in this area between the Neuse and Cape Fear rivers (Fig. 1). But again, until the relationships of these species are better known, it is impossible to provide a finer division of the Southern Atlantic Province.

CONCLUSIONS

The high degree of faunal heterogeneity among river systems illustrates the remarkable radiation that has occurred within North American freshwater mussels. Patterns of similarity among faunal regions and provinces shed light on the historical development of this fauna by suggesting the degree of past or present connectivity between river systems. Distributional patterns and relationships among mussel faunal groups are highly concordant with patterns for freshwater fishes, including the presence of similarly distinctive fish faunas in nearly all of the faunal provinces identified here for mussels (e.g. see Hocutt & Wiley, 1986). The similar distributional patterns between mussels and fishes reflect common responses to historical drainage evolution as well as the direct relationship between fishes and mussels whose larvae disperse on fishes (e.g. Watters, 1992).

Although the results of this study suggest past mechanisms of dispersal and vicariance, conclusions about these mechanisms are limited by the absence of a phylogenetic component in the dataset. The presence/absence nature of the dataset does not reflect phylogenetic relationships among populations of species in different river systems or among sister taxa, but these relationships are of central importance in identifying suites of species that have a common biogeographical history (Moritz & Faith, 1998). Phylogeographical studies of other aquatic organisms, including fishes (e.g. Strange & Burr, 1997; Near *et al.*, 2001; Berendzen *et al.*, 2003) and salamanders (Kozak *et al.*, 2006), have provided important tests of earlier hypotheses about the evolution of aquatic assemblages in North America. These studies, along with results for terrestrial organisms, have identified a number of recurrent biogeographical patterns in North America that coincide with distributional patterns of mussels (e.g. distinctiveness of the Interior Highlands and the faunal break between the Atlantic and Gulf of Mexico; see Soltis *et al.*, 2006). Phylogeographical studies have only now begun for freshwater mussels (e.g. Burdick & White, 2007) but will be essential to a better understanding of the evolution of the North American mussel fauna.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of drainage units used to examine patterns of freshwater mussel diversity and faunal affinities, with sources for distributional information within each unit.

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BIOSKETCH

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