Phylogenetics and North American Freshwater Fishes

Brooks M. Burr and Richard L. Mayden

The fresh waters of North America contain the greatest temperate fish fauna in the world. At least 1,061 species placed in 201 genera and 50 families have been recorded from 15 inland water faunal provinces. A compilation of the 979 taxonomically described species native to North America is presented by Mayden et al. in Chapter 29. This large assemblage compares with about 230 freshwater species in Australia, 250 in Europe, 1,500 in Asia, 1,800 in Africa, and 2,200 in South America (Gilbert, 1976). Although the fauna is of only moderate diversity relative to some other continents, numerous contributions over the last 200 years have detailed a wealth of knowledge about the distribution and biology of North American fishes. In recent years, two significant publications, the Atlas of North American Freshwater Fishes (Lee et al., 1980) and The Zoogeography of North American Freshwater Fishes (Hocutt and Wiley, 1986), have synthesized many previous labors and provided new and insightful information. Individual contributors to both volumes offer a review of biogeographical, ecological, and systematic information on fishes, and detailed coverage of historical geology of areas and rivers. A direct result of these two monumental efforts has been the realization that an incredible volume of data is presently available for the Neotropical fauna, making it a primary candidate for fundamental investigations in comparative biology.

These reviews also have revealed the fact that for many groups of fishes we lack elementary knowledge concerning their evolutionary histories, and much of the information available is rudimentary in nature. It is true that all known species have been classified and their classifications have been stable for many years. The basis for many of these classifications, however, has not been genealogical. For the most part, species and higher groups have been classified on the basis of overall similarity and magnitude of morphological affinity or distinctiveness. These classifications are not without merit and many will undoubtedly withstand the test of time.

Because of the paucity of phylogenetic hypotheses of species relationships our previous inferences concerning the evolution of the North American fish fauna have been indirect at best (Mayden, 1987a, b). Species relationships form an integral part of much of evolutionary biology. Investigations concerned with scenarios of historical biogeography, origins of communities, the evolution of complex feeding associations and behaviors, species associations, age of taxonomic groups, or origin of the North American fauna are all questions of an historical nature that demand some type of temporal information to provide direct estimates of history.

The taxonomic and ecological diversity exemplified in the North American fish fauna offers opportunities to address pertinent questions in comparative and evolutionary biology. Progress in these areas, however, is inherently constrained by and directly related to our progress in the development of phylogenetics. Consequently, development in this frontier is greatly dependent upon the advances made by systematists and the interchange between systematics and ecology, two historically independent fields. Presented here is a synopsis of the diversity of extant North American freshwater fishes, an abbreviated treatment of fish faunal provinces, and a review of the hypothesized relationships of component species.

DEFINITIONS AND METHODS

North America is defined here to include areas north of about 18°N on the Atlantic and 16°N on the Pacific slopes of Mexico (after Miller and Smith, 1986). The most southerly drainages on the Atlantic Slope is the Rio Papaloapan; on the Pacific Slope the Rio Verde/Atoyac forms the southern terminus.

Exotic and transplanted species are not included here. Most of the discussions dealing with systematics include only historically extant species; our inventory of fossil taxa is limited to those that are related to and included in phylogenetic analyses reviewed for extant species groups.

Freshwater fishes include, with a few exceptions, those that spend their entire lives in freshwater habitats, those living in marine water but reproducing in fresh water, or those capable of crossing narrow brackish or marine barriers. Except for species in which their ancestors are presumed to have been freshwater inhabitants (e.g., some species of Atherinidae, Fundulidae, and Cyprinodontidae (Mayden et al., Chapter 29; Table 3), we have eliminated all groups or species that are primarily brackish or estuarine. Exceptions include the enigmatic Ancorhinus mitchilli, the gilthead Microgadus tambaqui, the bronzed Serrasalmus marina, the syngnathids Heteropus brasiliensis, Pseudopontinus starkii, and Symphysodon aequispinna, the eels Electrophorus electricus, D. maculatus, Eleotris pilosa, E. ocellata, Gobiosoma dambii and G. polylepis, the garpike Arius leptostomus, A. anatolicus, Gymnogobius clarki, Bacteriocephalus neohoplopus, Gobiosoma atromaculatum, Sphyraena oxyacanthus, and S. canicula; the sea lampreys Lepidesthes multiscutatus and the soleids Triglops fuscans and T. macropterus; because some populations of these species are capable of maintaining their lives in fresh water (Reed, 1954; Radke, 1966; Ulmer, 1977; Miller and Smith, 1986; Mettee et al., 1987; Roesch, 1989; Swift et al., 1989; C. R. Gilbert, pers. comm.); E. L. Pesole, pers. comm.). Species representing the families Petromyzontidae, Acipenseridae, Anguillidae, and some members of the Clupeidae, Osmeridae, Salmonidae, and Mogurnda regularly complete parts of their life cycles both in fresh
and saltwater habitats and some species of each (except Anguillidae) are confined to fresh water. As with the array of data sets employed in systematic studies, several methods of analysis have been used to reconstruct the relationships of North American fishes. This symposium volume seeks to examine the significance of phylogenetic histories of fishes, in particular with respect to understanding the origins and evolution of particular aspects of their biology. Thus, systematic relationships discussed here include those presented in a phylogenetic (or cladistic) perspective sensu Hennig (1966). These include those that employ traditional Hennigian methods described by Wiley (1981), Eldredge and Cracraft (1980), and Nelson and Platnick (1980), or computer assisted phylogenetic hypotheses in the form of Wagner trees searching for maximum parsimony after Kluge and Farris (1969), Farris (1970), Swoford (1981, 1985), and Swoford and Olsen (1990). Although the philosophy of some analytical methods is controversial (Curello et al., 1984), hypotheses formulated using compatibility analysis (Estabrook et al., 1977; Estabrook 1984; Mescham, 1984) and maximum likelihood methods (Felsenstein, 1983) are also included. Many other contributions exist for North American fish groups wherein "relationships" of species or populations are presented. In these, however, exact methodologies used in developing hypotheses of relationships are lacking or the methods used were not developed to estimate histories, thus precluding the formulation of genealogical estimates. While we are aware that these efforts offer general information about the fauna, they are excluded from this review.

Literature in the systematic synopses includes only published documents having received peer review. Not included are theses, dissertations, or abstracts. While in most cases these investigations include valuable information about the North American fauna, they are nonetheless excluded so as to provide consistency in the available information base.

COMPOSITION AND DERIVATION OF THE NORTH AMERICAN FISH FAUNA: AN OVERVIEW

The origin and composition of the fossil and recent Neartic fish fauna has been the subject of several reviews (e.g., Darlington, 1957; Miller, 1959, 1965; Myers, 1966, 1967; Gilbert, 1976; Patterson, 1981; Smith, 1981; Briggs, 1986; Cavender, 1986; Myrle and Cech, 1988). In these compilations, general patterns of diversity within North America are noted and the origins of the fauna are discussed. Traditionally, researchers seeking explanations for these patterns have followed a research paradigm of centers of origin and dispersal, and prior to about 1970, were influenced by the fixed continent theory (e.g., Darlington, 1957). Areas of origin for dominant groups were usually identified as: 1) areas with the greatest species diversity; 2) areas where "primitive" or relict taxa existed; or 3) areas where the oldest fossils were found. In all of these studies except Patterson (1981), limited information was available on phylogenetic relationships of species or genera within or between continents. Consequently, multiple dispersal routes from Europe, Asia, or South America were invoked to account for existing ichthyofaunal diversity in North America. In a number of instances, fossil data were employed and precise times of colonization were identified. For some groups such as the gars (Wiley, 1976) and pikes (Nelson, 1972), dispersal explanations were justified and represent first-order explanations (sensu Wiley, 1986a) because phylogenetic relationships of species were available to test geographic relationships. For many other groups, however, where species relationships are unknown or not clearly documented with a distinct methodology, the biogeographic scenarios presented may not be justified. In a landmark paper, Patterson (1981) evaluated many previous scenarios for the North American ichthyofauna and concluded that without knowledge of phylogenetic relationships and a biogeographic approach seeking first-order explanations, little can be said about many of the potentially most informative groups of North American fishes (e.g., cyprinids, catostomids, icthyorids, salmonids, centrarchids) because knowledge of the systematic relationships outside North America is rudimentary. Because this kind of data has been only slowly forthcoming, previous theories about the historical biogeography of these important fish groups have been vague.

The recent treatise entitled The Zoogeography of North American Freshwater Fishes edited by Howett and Wiley (1986) reviews in detail the distribution and diversity of Neartic fishes. At the time most of the chapters for this book were written, there were still only a few phylogenies available for native fish groups. Subsequent to the submission of this book for publication, several papers have appeared in which the distributions of Neartic freshwater fishes are explained in light of genealogical information. These include Wiley and Mayden (1985) on speciation patterns, Mayden (1985b, 1987a, b) on biogeographic relationships of the Central Highlands fauna, and Mayden (1988a) and Nelson and Ladiges (1991) on endemic Central Highlands fishes wherein species are treated as characters and drainages as evolutionary units.

FAUNAL COMPOSITION

North America has a moderately rich freshwater fish fauna composed of at least 1,661 species representing 50 families and 201 genera (Table 1). Eight families and 128 genera (Table 2) have an exclusive North American distribution and probable origin. The endemic families include: Hiodontidae (2 species), Ictaluridae (48 species), Percidae (2 species), Aphyonidae (1 species), Ambloplitidae (6 species), Gomphidae (46 species), Centrarchidae (32 species), and Elassocephalidae (6 species). The Centrarchidae may not be endemic because Stentor (1960) reported eolophus (some putative Lepomis) from Eocene deposits of Europe. The Hiodontidae also may not be endemic as fossils purported to represent a new group (Hiodonmio) have been described from the Cenozoic of China (Li, 1987). Although Aplectidae is now restricted in distribution to eastern North America, fossil taxa placed in this family are also known from Europe, Asia, South America, and Africa (Cavender, 1986; Patterson and Longbottom, 1989); we therefore do not consider the family endemic to the Neartic realm.

There are two basic types of fishes found in fresh water, euryhaline marine fishes, and obligatory freshwater fishes (Myrle and Cech, 1988). Within the latter category, freshwater dispersants and saltwater dispersants can be recognized. Freshwater dispersants belong to families whose members are largely incapable of travelling long distances through salt water and include the primary and secondary freshwater fishes of Myers (1951). We have not followed the traditional classification of freshwater fishes as advocated by Myers and used by numerous authors because many primary
freshwater fishes have been shown to be tolerant of a wide range of salinities, and the distribution patterns of secondary freshwater fishes can often be better explained on the basis of local distance dispersal than on the basis of long-distance dispersal through salt water (Rosen, 1974, 1975). The division is not absolute and is somewhat arbitrary, but based on North American freshwater fishes and their abilities to disperse we consider over 95% of the included species in 30 freshwater dispersal,
Table 2. Composition of freshwater fishes of North America.

<table>
<thead>
<tr>
<th>Family</th>
<th>Genera</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Native Forms</td>
<td>50</td>
<td>1,063</td>
</tr>
<tr>
<td>Number of Endemics</td>
<td>8</td>
<td>966</td>
</tr>
</tbody>
</table>

and the majority of the remaining members in 20 families as saltwater dispersants. Of the freshwater dispersants, the bulk are members of the Cyprinidae (34%), Percidae (18%), Catostomidae (8%), Poeciliidae (8%), Ictaluridae (5%), Goodeidae (5%), and Fundulidae (4%); 8 of the saltwater dispersants must belong to the Salmonidae (28%), Atherinidae (14%), and Petromyzontidae (14%). The six dominant families, arranged in order of diversity, are the Cyprinidae (301 species), Percidae (165), Poeciliidae (75), Catostomidae (70), Ictaluridae (48), and Goodeidae (46); in total, they include 706 species or 67% of the fauna. The Cyprinidae and Percidae contain 467 (44%) of the 1,061 native species in the Neotropical Region. Polyodontidae, Anostidae, Anguillidae, Engraulidae, Aplocheilidae, Lotsidae, Gadidae, Pimelodidae, Sciaenidae, Cichlidae, Synbranchidae, and Pleuronectidae are each represented by either one extant species or one freshwater representative in our region.

A large assemblage of fish species of marine derivation has been recorded from North American fresh waters. Included in this category are the following 45 families and some 196 species (common name of family and numbers of species recorded from continental waters are in parentheses; families are listed in phyletogenetic sequence following Lauder and Liem (1983) and Moser et al. (1984): Elopsidae (Tarpons, 3), Aleuroidae (Bonefishes, 1), Ophichthidae (Snake Eels, 3), Engraulidae (Anchovies, 17), Clupeidae (Herring and Shads, 7), Osmeridae (Smelts, 3), Channidae (Fishi, 1), Ariidae (Sea Basses, 13), Synodontidae (Lizardfishes, 2), Gadidae (Codfishes, 1), Merluccitidae (Hakes, 1), Bathydraconidae (Tunnfishes, 1), Gobionocidae (Clingfishes, 1), Scomberesocidae (Sailfishes, 1), Belonidae (Needlefishes, 1), Hemiramphidae (Halfbeaks, 2), Atherinidae (Silversides, 6), Symphathistidae (Pipefishes and Seahorses, 2), Scorpaenidae (Scorpionfishes, 4), Triglidae (Scorplings, 1), Cottidae (Sculpins, 3), Hexagrammidae (Greenlings, 1), Tetraodontidae (Pufferfishes, 2), Centropomidae (Snooks, 5), Gobidae (Mugjack, 1, Echoppsidae (Spadefishes, 1), Lutjanidae (Snappers, 7), Pomadasyidae (Grunts, 11), Sparidae (Porgies, 2), Sciaenidae (Drums, 23), Carangidae (Jacks, 10), Mugilidae (Mullets, 2), Polynemidae (Threadfin, 2), Embiotocidae (Surfperches, 6), Dactyloptocidae (Sand Stargazers, 1), Uranoscopidae (Starfishes, 1), Pholidae (Gurneys, 1), Eleotridae (Sleepers, 1), Gobiidae (Gobies, 22), Trichonotidae (Cuskfishes, 1), Scorpididae (Mackerels, 1), Stomatomidae (Bitterfishes, 1), Bothidae (Lefroye Rounders, 6), Pleuronectidae (Righteye Rounders, 4), Soleidae (inclusive of Cynoglossus) (Sole and Tonguefishes, 5).

Some of the above-mentioned species (or a population of a given species) may eventually be found to reproduce or live out their lives in fresh water. Indeed, other members of 16 of these families have been shown to be freshwater fishes (Table 1). Except for elimination of the 19 or so species of clsoebranchs that have been recorded from North American fresh waters, the paucity of information on the fundamental life histories of the remaining species precludes accurate categorization other than reference to them as euryhaline marine groups. For more information on these species the reader is referred to the coastal faunal chapters in Hocutt and Wiley (1986) and species accounts and references in Lee et al. (1980).

Over the North American continent as a whole there are major differences in species diversity. For example, Canada and Alaska account for well over half the continental land mass but have only a small percentage of the species (less than 20%) and only about 10 fishes are restricted to that huge area (mostly salmonids) (Gilbert, 1976). Phenetically, the North American fauna can be divided into two obvious units, one western and one eastern. The two areas have distinctive faunas and are thought by some to have separate origins, Asian and European respectively. Most of the species are endemic to drainages east of the Rocky Mountains; only about one third of the diversity occurs west of the Continental Divide.

In eastern North America the fauna is dominated by a few genera (e.g., percids genus Etheostomes with 121 species, cyprinids genus Notropis with 75 species) and many species are endemic to single river drainages or basins. Much of the eastern diversity includes species of Cyprinidae, Percidae, Centrarchidae, and Ictaluridae. In contrast, the western fauna is somewhat impoverished, with fewer than 300 species (Gilbert, 1976). Historically this fauna was larger, if fossil taxa are included (Smith, 1981; Cavender, 1986) but the ichthyofaunal diversity of eastern drainages was apparently never achieved. The western fauna also differs markedly in composition. Major faunal elements include distinctive cyprins (e.g., Leptonema, Pogotoma, Ptychocheilus, Gilia) and catostomids (e.g., Chasmistes, Deltistes, Xyrauchen) genera and species of the families Salmonidae, Cyprinodontidae, and Cottidae.

Gilbert (1976) stated that in terms of origin the Neotropical freshwater fish fauna could be divided into six groups: 1) species from Europe and Asia; 2) North American autochthonous groups; 3) groups of marine origin; 4) those species that have invaded from Central America; 5) those invading from South America; and 6) relic archaic groups now largely restricted to North America. While phyletogenetic analyses are needed to verify theories regarding the origin of the North American fauna, it was suggested by Gilbert (1976) that the Cyprinidae, Percidae, Catostomidae, Esoxidae, and Umbelidae are of Eurasian origin; that eight families (see above) originated in North America; that the Poeciliidae are of Central American derivation; that the Cichlidae, Characidae, and Pomatomidae have reached the Neotropical region through relatively recent dispersal northward; and that the archaic Acantheporidae, Polyodontidae, Lepomisidae, and Amiaidae have a mixed origin; and that the remainder of the families are of marine origin. Patterson (1981) provided alternative hypotheses to those of Gilbert (1976) but concluded that cladistic information for many groups of plants and animals should be integrated before anything decisive can be said about the origin of the North American fish fauna.

FAUNAL PROVINCES

The full fauna of the Neotropical Region can be divided into 15 provinces (Fig. 1) that for convenience follow those recognized in Hocutt and Wiley (1986), except that the Mississippi Basin fauna and several distinctive drainages of the western United States are not subdivided. Provinces are treated in a north-to-south manner. The Yokom/Mackenzie Province covers all drainages of mainland North America tributary to the Arctic Ocean (east to McNeil Peninsula), to the Bering Sea, and to the Gulf of Alaska north of Stikine River (Lindsay and McPhail, 1986). Included in this province are 65 valid species in 14 families and at least three nominal salmonids and one lamprey of confused taxonomic status. As might be expected, the fish fauna is...
Phylogenetics and North American Fishes / 27

dominated by cool-water fishes including the Salmonidae (24 species) and Osmeridae (4 species), although 13 cyprinids are found in the area. As with the Hudson Bay Province, many of the primary freshwater fishes have invaded from the Mississippi Province or from more southern Pacific region. This province could be regarded, in part, as transitional between the Paleartic and Nearctic realms because the Alaska blackfish (Dallia peltata), Innocentia (Stenodus leucichthys), Arctic cisco (Coregonus artedi), least cisco (Coregonus artedi), and Arctic lamprey (Lampetra japonica) are otherwise found mainly in Siberia.

The Arctic Archipelago Province, the group of large islands north of Canada’s mainland, drains 1,500,000 square kilometers (581,444 square miles) (Crossman and McAllister, 1986) and contains the smallest fauna in the Nearctic Realm. Excluding Greenland, the Archipelago is the northernmost land of the continent and extends to within 800 km (500 miles) of the North Pole. Only eight species in three families are found in the area, including five salmonids, one cottoid, and two gasterosteids. No freshwater dispersants and no endemic species are yet known from the region, although some genetically differentiated populations that may have evolved postglacially from marine stock are present (Crossman and McAllister, 1986). Similar to the Hudson Bay Province, much of the area was glaciated during the Wisconsin Period and this in combination with salinity and climatic barriers account, at least in part, for the depauperate fauna.

The Hudson Bay Province, a huge area draining 4,000,000 square kilometers (1,547,474 square miles), contains all drainages of Hudson and Ungava bays in the north-central United States and much of Canada (Crossman and McAllister, 1986). The fauna shows strong affinities with the Mississippi and Great Lakes provinces and contains 101 species in 19 families. No species are endemic to the area, and many occur only at the southern edges of the province. As a result of Pleistocene glaciation, the fauna has occupied the province for less than 14,000 years. The distribution patterns of fishes reflect mainly the postglacial reinvansion of these drainages with dispersal through glacial lakes and rivers, shifting watersheds, and coastal waters (Crossman and McAllister, 1986).

The Great Lakes/St. Lawrence Province has several connections to the Mississippi River basin during times of glaciation and it is not surprising to find that its fauna is similar to that of the northern part of the Mississippi Province. A total of 168 species in 27 families is known from the Laurentian Great Lakes, the St. Lawrence River drainage, and the Atlantic drainage of Quebec, Labrador, and Newfoundland. The entire area was covered with ice of the Wisconsin age until about 15,000 years ago (Uličný and others, 1986). The Great Lakes do have a number of endemic forms, such as members of the Coregonus species complex and the blue walleye or blue pike (Stizostedion vitreum glaucum), but some of these are now extinct and the taxonomy of the whitefishes is confused to the extent that an accurate count of the number of species involved is difficult. The copper redhorse (Moxostoma hubbsi) is confined to the St. Lawrence River basin. The same group that dominate the Mississippi Province also dominate here, including Cyprinidae which accounts for nearly 30% of the fauna.

The Northern Appalachian Province includes Atlantic coastal drainages south of the St. Lawrence River through the Delaware River (Schmidt, 1986). One hundred six species in 27 families occupy the region. The Cyprinidae with 30 native representatives account for 29% of the fauna followed by Salmonidae (18%) and Percidae

Figure 1.
Faunal provinces of the Nearctic freshwater fish fauna. Number of families listed first, followed by number of species. Parenthetic figures represent percentual of species endemic to a given province.
Table 3. Basins, drainage, or region of significant endemic for North American freshwater fishes.

<table>
<thead>
<tr>
<th>Watershed</th>
<th>Number of Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mobile Basin</td>
<td>ca. 40</td>
</tr>
<tr>
<td>Tennessee R. Drainage</td>
<td>30</td>
</tr>
<tr>
<td>Rio Pinocho Drainage</td>
<td>29</td>
</tr>
<tr>
<td>Colorado R. Drainage</td>
<td>22</td>
</tr>
<tr>
<td>Rio Lerma-Santiago Drainage</td>
<td>17</td>
</tr>
<tr>
<td>Oroko Uplands</td>
<td>10</td>
</tr>
<tr>
<td>Columbia R. Drainage</td>
<td>13</td>
</tr>
<tr>
<td>Sacramento-San Joaquin R. Drainage</td>
<td>12</td>
</tr>
<tr>
<td>Cumberland R. Drainage</td>
<td>9</td>
</tr>
<tr>
<td>Roanoke James R. Drainage</td>
<td>8</td>
</tr>
</tbody>
</table>

(79%) Only one endemic, the nominal *Coryphaena foradii*, is known from the pre-Cambrian. As with other norther provinces all of the drainage in the northern Appalachian were inundated with ice and the native freshwater fish fauna has been formed from dispersal after recession of the ice.

The Cascadia Province lies west of the Continental Divide and is bounded on the south by the great Columbia River basin and to the north by the Skilak River (McKee and Linsey, 1968). Contains within these boundaries are 60 species placed in 11 families, making this province the most diverse in northwestern North America. Salmonidae (14 species), cyprinids (13), catostomids (11), and lampetra (6) account for the bulk of the diversity. Thirteen species are endemic to the Columbia River basin, including one of the two species of trout-perch (*Percinaidae*). A relative madison, *Novumbra phila*, occurs only in this province, and an endemic lamprey, *Lampetra nevadensis*, is restricted to Vancouver Island. Most of the rivers of Cascadia were covered by ice during the last glaciation, and their fish faunas were attained through postglacial dispersal largely from the Columbia basin.

The Mississippi province consists of all of the United States and Canada presently drained by the great Mississippi-Missouri-Ohio river basin. This province is by far the richest in North America with 675 species in 34 families. As expected, Cyprinidae (37%), Percidae (30%), Erimystidae (9%), Catostomidae (6%), and Centrarchidae (5%) predominate and together account for nearly 80% of the fauna. The Mississippi Basin has been important as a major center of fish evolution, as a refuge during times of glaciation, and as a refuge for representatives of past fish faunas. The Mississippi fauna is nearly the "mother" fauna of North America and much of the diversity of surrounding provinces can be accounted for by spillover from this cradle of temperate freshwater fish diversity. Important tributaries systems with high diversity faunas include the Tennessee River drainage with at least 30 endemic species (Table 3), the Cumberland River drainage with at least 9 endemic, and the Green River drainage with five. A physiographic region that is nearly restricted to the Mississippi Province (a few headwater streams of some Atlantic basins and Mobile basin tributaries are included), and generally termed the Eastern Highlands (Meyden, 1987a) is highly distinctive with 53 endemic species. The Oroko Uplands contain 16 endemic species. Among the most unusual fishes restricted to this province are the obligate cave-dwelling fishes *Amphodus* and *Stegophilobus*.

The Central Appalachian Province extends along the Atlantic Slope from the Susquehanna River drainage to the Edisto River drainage. Within this area, the known fish fauna consists of 177 species in 28 families. The most diverse families include Cyprinidae (59 species), Percidae (26), Catostomidae (18), Lota (12), and Centrarchidae (14). Diversity generally increases from north to south and reaches its peak in the Santanee-Pee Dee drainage with 96 species (including subspecies) (Houck et al., 1986). There are a number of drainage endemics including eight species known only from the James-Neosoke drainages and six from the Santanee-Pee Dee drainages. Nearly all of these are minnows, darters, suckers, and madtoms. The physiographic and geographic relics of Entomocera seminuda is endemic to tributaries of the Susquehanna River, Maryland. The reputed endemic fish fauna of Lake Waccamaw, North Carolina, while having a fair amount of recent ecological attention, is in need of systematic reassessment.

The Southeastern Province extends from the Savannah River on the Atlantic Slope to the Lake Pontchartrain drainages of the Gulf Slope. This province is second only to the Mississippi Province in diversity and contains 268 species in 31 families. In general, more species occur in northern Gulf Coast streams and in streams of higher elevation and usually of greater drainage area (Swift et al., 1986). The Mobile Bay Basin, numerically the third richest in North America, combines muddy lowland and upland species, including about 40 endemics. Upland endemics of the Mobile Bay Basin often share closest relatives with the diverse Tennessee River drainage fauna. Seven endemic species occur in the adjacent Apalachicola River and at least eight endemics occupy the Floridan area (Florida and nearby areas). The latter include one cyprinodontid (*Fundulichthys cornutus*), six fundulus (*Fundulus auratus*, *F. cumbensis*, *F. rubrofasciatus*, *F. similis*, *Leptolaemus occurus*, *Lucania goodei*), and one elassoma (*Elassoma octofasciatum*). At least 10 suckfish or marine species can be regularly encountered in fresh water. The fish faunas of this province is so distinctive that Swift et al. (1986) subdivided it into 10 subprovinces.

The Colorado Province is drained by the Colorado River basin which flows through some of the most arid and in western North America. The province is home to 32 species in 7 families, 22 (69%) of which are endemic to the basin (McClung, 1986). Among the more unusual faunal elements are six species (comprising three genera) in the endemic cyprinid group of spinedace, at least three species in the *Gila robusta* complex that live in the mainstem Colorado River, and the *Gila tolpotnus*, *Poteosilpis occidentalis*, which may have entered the basin from farther south in Mexico. The big-river fishes in the basin share an array of morphological adaptations that are seen nowhere else in the North American fauna. Many are large, including *North American* (Great crested, *Pharyngodon inclusus,* and some *Ponchosuchus tamarisci* and especially *Gila cyphus*) develop pronounced pronged humps or extremely thin caudal peduncles (e.g., *Gila elegans* and *G. cyphus*). The brilliantly-colored *Onychobrycon apogon* and *O. gracilis* are also endemic here.

The Great Basin-Baja California-San Francisco Province includes the 150 internal basins in the Great Basin, the Klamath and Rogue drainages on the California-Oregon boundary, the great Sacramento-San Joaquin basin of California, and numerous coastal drainages and endorheic basins of Oregon, California, and Baja California. All the sub-basins in the Great Basin are arid, although they were filled with large lakes during the Pleistocene (Haldin et al., 1974). Consequently, there is a highly endemic, but rather impoverished, fauna, for example, only 10 species in Death Valley, 13 species in the Lahontan system, and 20 species in the Bonneville system. Nearly 60%
of the species are either cyprinids or catostomids, although four pupfish, three goatfishes, and four whitefishes or ciscoes (genus Prosopium) occur in the area. About 80% of the species in the Great Basin are endemic (Miller, 1959).

The Klamath-Rogue drainages contain about 30 obligate freshwater fishes including four cyprinids, four suckers, four lampreys, eight salmonids, and six sculpins. Thirty-seven percent of the species are endemic to the drainage including all the suckers (Moyle and Cech, 1988).

The Sacramento-San Joaquin basin contains most of the water that flows in California, and includes at least 43 species, of which 42% are endemic (Moyle and Cech, 1988). Among the endemic forms are an unusual assembly of 10 minnow species and the only native centrarchid, the Sacramento Perch (Archoplites interruptus), west of the Continental Divide. Also noteworthy is the presence of the strikingly beautiful golden trout (Oncorhynchus aguabonita) and the tule perch (Hypostomus breviceps); the latter species is the only freshwater representative of the principally marine family Embiotocidae.

The Western Gulf Slope Province, including all Gulf Coastal drainages from the Calcasieu River to the Nuclear River, contains 132 species in 24 families. Eight of these fishes are confined to the Western Gulf Slope, among which six are drainage endemics. The dominant families in order of decreasing diversity are Cyprinidae, Percidae, Centrarchidae, Fundulidae, Catostomidae, and Ictaluridae. Compared with those of the central and eastern portions of the United States, the Western Gulf Slope ichthyofauna is somewhat depauperate (Conner and Suttkus, 1986). Unique ichthyofaunal elements include the bizarre subterranean Ictalurus saltans and Tingiopleuron, three endemic Gambusia, and the most northern native populations of the largely Mexican characin, Astyanax mexicanus.

The Rio Grande Province consists of several interior basins of north-central Mexico that were formerly connected to the Rio Grande (e.g., River Nazas and several other Chihuahuan desert streams) and two independent streams of northeastern Mexico, the rio San Fernando and Soto La Marina, which share many fishes with the Rio Grande (Smith and Miller, 1986). The known native fish fauna consists of 134 species in 21 families. Included are five Nearctic or Holarctic families, Cyprinidae (41 species), Catostomidae (10), Ictaluridae (10), Centrarchidae (5), and Percidae (6), but only two Neotropical families, Characidae and Cichlidae, which provide only three species. A high degree of endemism characterizes the fauna, with 50% of the species confined to the province, most in the genus Notropis and some 30 of which are cyprinodontoids, many of which are found in isolated springs. According to Smith and Miller (1986), this endemism has been strongly influenced by disruption of the hydrographic system into numerous disjoint basins. An unusual faunal element is the blind catfish, Pterichthys.

The Sonoran-Sinaloa Coastal Province extends from the northwestern corner of Mexico along the Pacific Slope to the Rio Grande de Santiago. The fauna is depauperate compared to the Rio Grande and Central Mexican provinces with only 45 species representing 15 families. Twelve cyprinids, eight pycnocephalids, and seven catostomids account for 60% of the diversity. A large number of species (125 in 37 families) of marine derivation, however, are found in the lower reaches of the drainages (Minksley et al., 1986).

The Central Mexican Province is the most southern province recognized in the Nearctic Realm and extends from the Rio Pánuco to the Rio Papaloapan on the Atlantic Slope and the Rio Grande de Santiago to the Rio Verde/Atayac on the Pacific Slope (Miller and Smith, 1986). Twenty-five families with 205 species occupy the province (Miller, 1986; Miller and Smith, 1986; Rauchenberger et al., 1990). While cyprinids, catostomids, and loaches comprise nearly 20% of the fauna, the most diverse ichthyofaunal elements in the province include the goatfishes (29 species), poeciliids (43), and atherinids (38). Other noteworthy types for the Neotropical Realm are an arid zone that lives chiefly in freshwater, three pelidromies, one freshwater belonid, two rivulines, 13 cichlids, and one swamp eel. There has been an explosive radiation among the goatfishes and the atherinid genus Chirostoma, including many species now restricted to lacustrine environments. Two basins found in this province have unusually high numbers of indigenous species; these are the Rio Pánuco with 29 and the Rio Lerma-Santiago with 17 endemic species (Table 3).

PHYLOGENETICS OF THE FAUNA

The application of phylogenetic methods to the native North American fish fauna has occurred only recently, beginning in 1969. Explorations and descriptions of the fauna prior to the development of phylogenetic theory account for most of what is presently known about the diversity, distribution, origin, and relationships of the species. In fact, most of our existing classification for these fishes was developed by prominent ichthyologists working under a different evolutionary and systematic paradigm than that advocated today. Major contributions by such luminaries as C. S. Rafinesque, C. A. Lesueur, L. Agassiz, C. F. Girard, S. F. Baird, T. N. Gill, R. D. Cope, D. S. Jordan, H. W. Evermann, C. H. Gilbert, C. H. Eigenmann, S. E. Mook, S. E. Hildebrandt, H. W. Fowler, C. L. Hubbs, H. E. Raney, D. E. Rosen, and their students supply an invaluable knowledge base for the fauna.

Previous systematic methodologies, not just in ichthyology, have historically been criticized by researchers from other scientific arenas as being purely descriptive and lacking in testability. In recent years, some have become aware of these criticisms and are beginning to develop methods for developing rigorous tests of hypotheses. Although a difficult job, the application of these methods to systematic problems among North American fishes is a promising undertaking.

Because of the relative paucity of applying phylogenetic methods to the Nearctic fish fauna, only a moderate number of studies exist in which specific hypotheses, supported by evolutionary innovations, are presented. The educational development of Hennigian methods in North America can be traced largely to the ichthyologist Gareth J. Nelson of the American Museum of Natural History and the Entomologist Herbert H. Ross (1908-1978). Nelson essentially brought phylogenetic philosophy to New York and the New World from Europe in the late 1960s and
actively supported the spread of these ideas (Hull, 1988). Ross, then at the Illinois Natural History Survey, was essentially practicing the methods espoused by Hennig and Brunius, and was instrumental in the publication of the translated version of Phylogenetic Systematics at the University of Illinois.

Since 1969, when the first publication using phylogenetics on North American fishes appeared, there has been a steady increase in the general appreciation, understanding, and application of these methods (Fig. 2). In fact, this is evidenced today by a nearly universal application of these techniques when genealogical relationships of species are being sought. It is not to say that the many phenetic studies of North American fishes did not contain hypotheses of relationships. In fact, many previous concepts of groupings have withstood recent phylogenetic revisions. Other species relationships, however, were based strictly upon overall similarity without reference to similarities that were the result of retained primitive traits. Likewise, other concepts of relatedness were commonly based on the observation of “groups” and “not groups” wherein lineages could be defined on the basis of either having a character or not having the character. In many of these instances it is clear that members of one group are not each other’s closest relatives, whereas members of the other are descendants of a single common ancestor. Thus, the previous literature may contain taxa of mixed origin, especially where methods are not explicit.

One of the consequences of the relatively uniform acceptance of phylogenetics is the necessity to recognize historical connections between species and relay this information in a consistent classification (Chapters 4 and 29). Some have interpreted the necessity to recognize historical connections between species and relay this information in a consistent classification (Chapters 4 and 29). Some have interpreted the taxonomic relationships in several instances of several species in the North American freshwater fishes to be monophyletic and the sister to the fossil family Chondrosteidae.

A SYNOPSIS OF PHYLOGENETIC STUDIES

Petromyzontidae—Lampreys

No phylogenetic analyses of the Neartic lampreys are available, although lampreys have been the subject of a number of recent ecological and taxonomic studies. We recognize 21 species in only three genera (sensu Bailey, 1980) (although see Chapter 29 for nominal forms). Until a more comprehensive investigation of lampreys is completed, the genera Lethenteron, Telopistodon, and Entosphenus are considered synonyms of Lampetra; their application may be appropriate in future phylogenetic studies. Eleven of the 21 species are nonparasitic; the remaining species are well known for their parasitic habits. The phenomenon of paired or solitary species (Vladikov and Kott, 1979), in which the often sympatric living nonparasitic lampreys are considered to be derivatives (descendants) of living parasitic lampreys (ancestors), is unique among vertebrates and warrants a rigorous test using a phylogenetic approach.

Acipenseridae—Sturgeons

Sturgeons are widely distributed in the Northern Hemisphere, and exhibit either an anadromous or wholly freshwater life cycle. Some sturgeons rank among the largest of freshwater fishes—up to 20 feet (6.1 m) in Acipenser transmontanus of the North American Pacific Coast. Overfishing, pollution, and habitat destruction have all contributed to the decline in the commercial importance of North American sturgeons. Slow growth and late maturity make sturgeons especially vulnerable to overharvest. Of the 23 species, eight are represented in North America in the genera Acipenser and Scaphirhynchus. Five of the eight species are considered endangered or threatened (Williams et al., 1989). Nelson (1966a) placed sturgeons and paddlefishes together as sister groups. Patterson (1982) and Lauder and Liem (1983) considered the sturgeons to be monophyletic and the sister to the fossil family Chondrosteidae.
Polyodontidae—Paddlefishes

In appearance and habits the paddlefish, Polyodon spathula, is one of the most unusual faunal elements found in North American freshwater species. Although it is one of the larger (to 221 cm [87 in.]) freshwater fishes in North America, it feeds principally on microscopic organisms throughout its life. The long paddle-shaped snout, covered by an elaborate system of sense organs, perhaps aids the fish in locating concentrations of food organisms.

Patterson (1981) presented relationships among members of this family. The two extant species, *P. spathula* and *P. acutus*, comprise a monophyletic group, sister to the fossil genera *Cassuthus* and *Paliopsaurus*. Gardiner (1984) agreed with Patterson that *Cassuthus* was the sister group of the extant paddlefishes, but assigned *Paliopsaurus* as the sister group of *Acipenseridae*. The family was considered monophyletic and sister to a monophyletic group inclusive of *Acipenseridae* plus Chondrosteidae by these authors and Lauder and Liem (1983). Gardiner and Semis (1991) evaluated extant fossil and recent materials for paddlefishes and phylogenetic relationships of Polyodontidae to Chondrosteidae and Acipenseridae. These authors found little support for previous concepts of relationships of paddlefishes. Instead they argued that the family was the sister group to Acipenseridae and this clad was in turn the sister to Chondrosteidae. Within the family, *Polyodon* formed the sister to *Cassuthus*. This clad, sister to *Paliopsaurus*, was the sister group to *Paliopsaurus*.

Lepisosteidae—Gars

The piscivorous gars occupy large bodies of water, and are often found resting in loosely formed groups just under the water's surface. The ability to gulp atmospheric air permits gars to survive in waters so low in oxygen as to be unsuitable for most other fishes. Relationships, monophyly, and biogeography of fossil and Recent species of gars were discussed by Wiley (1976). The family contains two genera, *Lepisosteus* and *Atractosteus*, and seven Recent species (five in North America), and is the sister group to the Halecomonti (Wiley, 1976; Wiley and Schultze, 1984). A tree based on cyto genetic data and showing the same relationships of major groups as in Wiley (1976) is given in Dingerkus (1979). An earlier study (Nelson, 1964a) placed *Lepisosteus* and *Amia* together as sister taxa (the former Holostei, in part). Based on unpublished data and the fossil genus *Watsonius*, Olsen (1984) hypothesized that fossil gars were more closely related to teleosts, including a clad of the fossil genera *Macrosemius*, *Dapedium*, *Philodus*, and *Leptiolus*, than to Amiaidae.

Amiaidae—Bowfins

Only one extant species, *Amia calva*, is known. The reproductive habits of the bowfin are unusual among primitive Neartic fishes in that males build and defend nests and continue to guard and defend schooling young for a period after hatching.

Wiley (1976) and Dingerkus (1979) considered Amiaidae the sister group to teleosts, whereas Nelson's (1964a) work on gill arches placed Amia and Lepisosteus together as sister groups. Lauder and Liem (1983) included the Amiidae, plus two fossil families, as sister to Teleostei. Patterson (1973, 1981), Olsen (1984), Schultze and Wiley (1984), Bryant (1987), and Patterson and Longbottom (1989) provided a phylogeny and/or classification for this species and fossil relatives. Olsen (1984) summarized and interpreted characters, some previously unpublished, for Amia, *Lepisosteus*, and several fossil taxa. A subtree inclusive of Amia and *Cassuthus* forms the sister group to a monophyletic assemblage including other "caturids" such as *Iffeneuclidus*, *Ophiopsis*, and *Macropius*. Bryant (1987) also hypothesized a sister group relationship between Cassuthus and Amiaidae. Within the family, Amia forms the sister group to a clad inclusive of *Enneopterus*, *Mélisia*, and *Rhamphichus*. Patterson and Longbottom (1989) compared the differing hypotheses of Schultze and Wiley (1984) and Bryant (1987) and the distributions of the pertinent characters with new fossil information. These authors concluded that given the present difficulties in determining homologies and the unknown character conditions in some taxa, it is premature to conclude any scheme of familial relationships. An examination of 13 populations of Amia from the southern United States revealed two major genetic assemblages of mtDNA clades, as determined by a Wagner network (Bermingham and Avise, 1986; Avise et al., 1987).

Hiodontidae—Moneyes

Two species of the Osteoglossomorpha (genus Lauder and Liem, 1983), *Hiodon alosus* and *H. transpacificus*, occur in streams and lakes of North America. Fossil and Recent osteoglossomorphs are known from all continents except Europe; extant members of the group are now considered relics where they occur (Wilson and Williams, Chapter 6). In one of the first applications of a phylogenetic analysis to a North American freshwater fish group, Nelson (1969b) hypothesized a sister relationship of Hiodontidae to Notopidae. Greenwood (1970, 1973) and Patterson and Rosen (1977) summarized relationships and placed the family as sister to Lycodontidae, and this clad in turn sister to Notopidae plus Mormyridae. Lauder and Liem (1983) corroborated these conclusions and supported the monophyly of Hiodontidae. Patterson (1981) also supported this phylogeny and placed Eohiodon as the sister species to the two North American species, Wilson and Williams (Chapter 6) reviewed the traditional relationships of *Hiodon*, *Eohiodon*, and Lycodontidae, but suggested that close relatives to the *Hiodon* plus Eohiodon clad exist in the Cretaceous and early Tertiary of China and the U.S.S.R. (see also Li [1987] for the closely related genus Vanbania in the Cretaceous of China). These authors also discussed the fundamental impact that fossil osteoglossomorphs and phylogenetics have had in interpreting the biogeography and evolution of life history traits of *Hiodon* and *Eohiodon*. *Hiodon* is apparently unique among osteoglossomorphs in the structure of its caudal skeleton (Schultze and Arratia, 1988).

Anguillidae—Freshwater Eels

*Anguilla rostrata* is the only member of the family in North American fresh waters. The species is catadromous, migrating great distances from fresh water to the
Sargasso Sea where adults apparently die after spawning, Smith (1984) discussed higher relationships within Anguilliformes and noted that the Anguillidae was morphologically distinctive. This family has no defined characters clearly relating it to any other anguilliform families. Anguilla contains at least 16 species (Nelson, 1984), but A. anguilla is considered to be the sister species, or perhaps conspecific with, the European eel, A. anguilla.

**Engraulidae—Anchovies**

New World anchovies, comprising some 80 species in nine genera, are mostly inshore marine fishes, but several species migrate up rivers, and some live permanently in freshwater (Nelson, 1984; Grande and Nelson, 1985). Most anchovies are abundant, small planktivorous carnivores and are among the most important commercial fishes (Grande and Nelson, 1985). One species, the bay anchovy (Anchoa mitsukurii), is common in lower freshwater and estuarine reaches of coastal rivers from Maine to Yucatan, Mexico. Recently, this species was reported from the lower Tombigbee River, about 271 miles inland from Mobile Bay (Mettee et al., 1987); we presume that these populations of this species live permanently in North American fresh waters (see Taggart, 1968). Nelson (1983) and Grande and Nelson (1985) showed that Engraulis (cosmopolitan distribution) and the New World anchovies (six genera) plus Engraulidochromis (2 species) form a monophyletic group, the Engraulinae. Relationships of A. mitsukurii to other Anchia are unknown.

**Clupeidae—Herring and Shads**

Ten clupeid species, a group of silvery, slender-bodied fishes, occur in North America; two of these are known only from Mexico and far southern Texas (Nelson, 1970) hypothesized phylogenetic relationships of genera in the family. Among North American genera, Alosa was sister to Sardinia (matriline, northeast Atlantic and Mediterranean), and Dorosoma the sister to Notropis (matriline, Indo-Pacific). Grande (1985) reevaluated previous statements of relationships and considered them largely unresolved (Grande and Nelson, 1985). Placement of Dorosoma and Alosa in the subfamilies Dorosomatinae and Alostinae, respectively, is largely for convenience, since none of these subfamilies are considered monophyletic (Grande, 1985).

**Cyprinidae—Minnows and Carps**

Minnows are the most diverse freshwater fish family in North America and are frequently used for bait and in aquaculture. A total of 402 described and undescribed species in about 50 genera are known from this continent. Many species are extremely colorful during the reproductive season and a variety of reproductive modes are known to exist across taxa. Several species exhibit relatively unspecialized spawning behaviors over the substrate, while other genera have specialized nest building or nest association behaviors (Johansson and Page, Chapter 22).

By far, most systematic studies involving a majority of North American cyprinids have employed morphological features, both internal (osteology, myology, digestive system, etc.) and external (meristics, morphometrics, tuberculosis, color, etc.). The application of molecular techniques is increasing, but fewer investigations have used protein electrophoresis, restriction-site analysis, sequencing, or a combined morphological/molecular approach. McAllister and Cojd (1978) described a novel, but questionable, approach for estimating descent and employed degree of hybridization between taxa as an indication of relatedness. Although several researchers have investigated cyprinid relationships, using a variety of techniques, much work is needed to resolve additional species relationships as well as the conflicting hypotheses of ancestry.

The minnow species of North America may not represent a monophyletic assembly. For many years Notemigonus was considered a member of a subgroup within the family primarily composed of Old World species (Miller, 1959). Howes (1981), however, found no evidence to relate this species to any Old World minnows (but see Cavender and Coburn, Chapter 9). In a phylogenetic analysis of relationships of the aspinine cyprinids, Howes (1984) further supported the polyphyletic origin of the New World fauna and related the western species Pimelochromis to the Asian genus Pimelodus. This aspinine group was also suggested to include Pimelochromis, Lavinia, Mylopharyngodon, and Gila (in part) of the North American fauna.

Cavender and Coburn (Chapter 9) and Coburn and Cavender (Chapter 10) investigated relationships of many New and Old World genera. These authors acknowledged a non-monophyletic North American assemblage and recognized two subfamilies in the family, including Cyprininae and Leuciscinae. Twelve tribes are described to the Leuciscinae, of which the phoxinines include nearly all North American species (except Notemigonus), the Holarctic Phoxinus, and some Asian genera. Notemigonus was considered to be related to the Eurasian leuciscins (Cavender and Coburn, Chapter 9). Coburn and Cavender (Chapter 10) placed all other North American species in three clades. These included a primarily eastern shiner clade, a western minnow clade, and a polyphyletic group including a primarily eastern chub clade and a western clade. The western clade included most western genera and did not contain the aspinine species of Howes (1981). Relationships in this clade are partially unresolved, and the genus "Gila" is polyphyletic; Pimelochromis, Lavinia, Mylopharyngodon, and Gila (in part) are part of a polyphyletous clade with other western genera; and Triops and Agonostoma are related to Rhynchocyphaeidae.

Other systematic analyses of the western fauna include one of the first studies within the family using phylogenetics. Species relationships within the genus Alasmus were described first by Barbour and Miller (1978) and later by Jensen and Barbour (1981). An early attempt at a phylogenetic analysis within this family also included a Wagner analysis of distance data for western genera by Avise and Avalos (1976). These authors employed alloxyn characters and midpoint rooting to determine relationships of some species of Gila, Hoplosternum, Pimelodus, Mylopharyngodon, Notemigonus, Orthodon, Pimelochromis, Pimelochromis, and Richardi. They also identified a sister group relationship between Notemigonus and the remaining taxa. Two phylogenetic hypotheses for species relationships of Pimelochromis were offered by Carney and Page (1980); Mayden et al. (1991) showed a sister group relationship between Pimelochromis and Mylopharyngodon and resolved relationships among species of Pimelochromis. Woodman (Chapter 11) analyzed species relationships within the
primarily western *Rhinichthys* and included both *Agosia* and *Tiarqua* in this genus. Mayden and Hills (1990) briefly discussed relationships of western members of the genus *Cynopterus*. Mayden et al. (Chapter 25) used allozyme electrophoresis to investigate species relationships in *Dionda* and resolved sister group relationships among *Dionda*, *Hybognathus*, and *Campostoma*.

Hypotheses of relationships for species of the diverse eastern cyprinid component are more numerous than those for western representatives. The earliest investigations distinguishing between primitive and derived characters in these species included compatibility analyses using allozyme characters by Buth and Burr (1978) for populations and species of *Campostoma*, and by Buth (1979a) for species relationships in *Lsuccina*. The relationships among and within many of the eastern cyprinid genera have been the focus of two general systematic studies by Mayden (1989) and Coburn and Caveneder (Chapter 10). Both analyses used morphological features and both were congruent in several recognized sister group relationships. However, some differences in composition of genera and relationships of genera do exist between these studies, as well as the resulting taxonomies.

Mayden (1989) examined species relationships within the genus *Cynopterus* and other genera. The taxa *Hybognathus* and *Notropis* as previously recognized were not found to comprise monophyletic assemblages. Several clades were recognized within a large clade of mostly eastern cyprinids, including *Erycynia*, *Hybognathus*, *Platygobio*, *Macobygnathus*, *Extrarius*, *Eoxoglossum*, *Phenacobius*, *Erimystax*, *Hybognathus*, *Campostoma*, *Dionda*, *Nocomis*, *Agosia*, *Oregonichthys*, *Pinguihales*, *Yuria*, *Richardsonius*, *Clinostomus*, *Paronotropis*, *Lythrurus*, *Lucius*, and *Notropis*.

Coburn and Caveneder (Chapter 10) examined additional genera in a more inclusive evaluation of the phylogeny of North American Cyprinidae. In addition to the western clade discussed above, they recognized a shiner clade and chub clade, both consisting mostly of eastern taxa. The chub clade included the genera *Tribolodon*, *Rhynchocheilus*, *Pentodon*, *Margaria*, *Semotilus*, *Platygybion*), *Hybognathus*, *Campostoma*, *Dionda*, *Macobygnathus*, *Erimystax*, *Nocomis*, *Eoxoglossum*, and *Phenacobius*. The shiner clade included the genera *Richardsonius*, *Clinostomus*, *Oregonichthys*, *Nocomis*, *Lythrurus*, *Cynopterus*, *Pinguihales*, and *Opsonopsocidae*. These authors included the genera *Pentodon*, *Hybognathus*, and *Erycynia* in *Notropis*, combined *Extrarius* with *Macobygnathus*, removed *Opsonopsocidae* from *Notropis* as the sister to *Pinguihales*, and preferred different species compositions for the genera *Cynopterus* and *Erimystax* and the subgenus *Paronotropis* and *Hybognathus*. We prefer to retain the genera *Erycynia*, *Hybognathus*, and *Paronotropis* to promote the preservation of information concerning relationships of included species. All of these groups are monophyletic and are not known to jeopardize the monophyly of *Notropis*.

Many other phylogenetic hypotheses exist for eastern cyprinid groups other than those presented by Mayden (1989) and Coburn and Caveneder (Chapter 10). Phylogenetic relationships of some *Ltehrurus* were investigated by Rogers (1984), and Stein et al. (1985). Species relationships within *Lucias* were presented by Wiley and Mayden (1985) and Mayden (1987a), and later modified by Mayden (1988a). Relationships of species within *Phenacobius*, *Erimystax* and *Erimomax*, *Pinguihales*, *Nocomis*, some *Cynopterus*, and some *Notropis* were presented in Mayden (1987a). Wiley and Mayden (1985) summarized relationships for *Erlymystax* and *Erimomax*, *Lythrurus*, and *Paronotropis*, as well as some *Hybognathus* and *Notropis*. Dimmick (1987), using allozyme data, evaluated relationships among species of *Paronotropis*. This analysis supported the inclusion of *P. welaka* in *Paronotropis*, but not *Notropis* *habba*, and a close relationship between *Opsonopsocidae* and *Cynopterus*, relative to other taxa examined. Hoyes (1985) argued for a monophyletic *Phenacobius*, sister to the genus *Conocilius*, and Starnes and Jenkins (1988) presented relationships for some eastern species of *Phaeomas*. A phylogeny of the *Notropis* *veluticeps* species group based largely on allozyme characters is presented by Mayden and Kuhlfeld (1989). Johnston and Ramsey (1990) offered a phylogeny of *Semotilus* and the former *Semotilus* (now *Margaria*) was not identified as a member of the ingroup. Alternate phylogenetic hypotheses among populations within the *Notropis* *chloropterus* species complex were recently summarized by Wood and Mayden (1992). Cook et al. (1992) provided a distance Wagner tree depicting relationships of several species of *Hybognathus* using allozyme electrophoresis; *H. amurus* was treated specifically distinct and as the sister group to three other *Hybognathus*.

The application of novel character types, including chromosomal attributes, endonuclease cleavage maps of mitochondrial DNA, and behavioral-ecological characters as information in formulating and testing phylogenetic hypotheses of cyprinids has been minimal. Only recently have these data and analyses been attempted and/or possible for species relationships. Gold and Amemiya (1986) and Amemiya and Gold (1988, 1990) provide cytological evidence, primarily NOR variation, for species relationships among several North American species groups and genera. Species phylogenies and many of the advances with the use of chromosomal banding and the interpretation of NOR variation are reviewed by Amemiya et al. (Chapter 19). Dowling and Brown (1989) inferred relationships of four eastern species, representing the clades *Notropis*, *Lucius*, *Hybognathus*, and *Pinguihales*, and found some resolution using allozyme data, but minimal phylogenetic information using mtDNA.

Hicks et al. (Chapter 19) studied variation in genome size and estimated rates of genomic evolution using a modified phylogeny from Mayden (1989). A tree including the genera *Cynopterus*, *Opsonopsocidae*, *Codoma*, and *Pinguihales* based on unpublished cytogenetical data was examined by Page and Cess (1989) to infer the evolution of some reproductive behaviors. In a follow-up analysis, Page and Johnston (1990) included a tree of the relationships of these same genera based on reproductive and behavioral characters. Accounts of the reproductive biology of representatives of these genera were in agreement with the tree topology. From an array of reproductive behaviors, Moutakis et al. (1991) provided a cladogram of relationships of three species of *Nocomis* using *Camposoma anamalum* as the outgroup. Finally, Heins and Baker (Chapter 21) employ reproductive parameters and paralogy analysis to reconstruct species relationships in the *Hybognathus dorsalis* species group.

**Catostomidae—Suckers**

This Holartic family contains 14 Recent genera and about 71 species, of which 13 genera and about 70 species occur in North America. Suckers are one of the dominant groups of large fishes in North America and often account for the greatest biomass in streams, lakes, and reservoirs. Some species form a major portion of the economically valuable catch of commercial fishermen.
The earliest attempts to unravel relationships of catostomid species using genetic data and a cladistic approach were those of Ferris and Whitl (1978) on most catostomid genera and Ruth (1979, c. 1980) on the tribe Moostostominae, the subgenus Thoburnus, and the genus Hypentelium, all western North American groups. Rogers (1984) and Swedlow and Berlocher (1987) ranalyzed the original Hypentelium data of Ruth (1980) as an example of a new tree construction method using data in the form of either frequencies or discrete characters. Fulman (1985) used developmental characters to produce phylogenies for 17 species of catostomids. The first Wagner tree generated for a North American freshwater fish group was by Smith and Koehn (1971) on western suckers of the genus Catostomus using genetic and morphological characters. Miller and Smith (1985) provided cladograms for fossil and recent species of Che chamistes, the suckers, and Minckley et al. (1986) modified the Smith and Koehn and Miller and Smith trees in their discussion of area cladograms and comparative geography of western fishes. G. B. Smith in Bockstein et al. (1985) produced a tree for relationships of all catostomid genera, the actual character data for this tree were not presented.

The most complete analysis of catostomid relationships, in terms of number of taxa and types of characters, is that by Smith (Chapter 28). A survey and review of numerous morphological and molecular characters and a phylogeny of 64 taxa (15 genera including the fossil Amyon) that was used to revise catostomid taxonomy and infer modes of speciation and patterns of biogeographic and ecological evolution. All previously recognized genera were found to be monophyletic except *Moostostominae,* which was rendered paraphyletic with the recognition of Hypentelium and Lagochilus. As a partial solution Smith (Chapter 28) synonymized Lagochilus and *Scantomyzon* from "Moostostominae," but recognized that "Moostostominae" and *Scantomyzon* were unnatural groupings. *Scantomyzon* amazonus is the sister group to Thoburnus plus Hypentelium.

**Characidae—Characin**

This diverse family is potently a monophyletic grouping, but hypotheses of specific relationships within the group are largely lacking. No phylogenetic hypotheses exist for the four North American members of this family. At present, the genus Astyanax is not considered a monophyletic assemblage since some species are probably more closely related to other genera than to congeners (Boesem, 1972; Weitzman and Strip, 1983). The genus Lebiasina, for example, is monophyletic and contains at least three species, *B. breviseta, B. buiylapi,* and *B. m. (B. cucullanus, R. R. Miller, pers. commun) (Miller, 1986);* the latter species, known from the Rio Papaloapan, is the only non-American representative. These species are most closely related to some species within Astyanax (Weitzman and Strip, 1983).

**Ictaluridae—Bullhead Catfishes**

The easily recognized North American catfishes are endemic to North American freshwaters, occurring primarily east of the Continental Divide (at least six species occur in Pacific drainages of Mexico). Forty-eight recent species are recognized, 27 of which are the diminutive madtom. The unusual blind catfishes in the genera Scaenops, Trogodina, and Priopella are denizens of subterranean environments of Texas and northern Mexico. A few of the larger catfishes (family Ictaluridae) are important sport, commercial, or aquaculture species of eastern North America.

Using Wagner methods and an osteological data set, Lundberg (1975) summarized the cladistic and chromatic relationships of fish and living Ictalurids, excluding *Troglostoma* and species relationships of Noturus. Several clades were shown, including one for Ictalurus (sensu stricto), the bullethead, the madtoms plus Priopella, and Satam plus Pylodictis. In 1982 these relationships were slightly revised to show that *Troglostoma* was sister to a clade including *Amia* and *Noturus,* plus *Priopella,* and *Satan* plus *Pylodictis.* In 1982 these relationships were slightly revised to show that *Troglostoma* was sister to a clade including *Amia,* *Noturus* plus *Priopella,* and *Satan* plus *Pylodictis.* Lundberg's (1982) classification included a redefinition of Ictaluridae and the sister group to all other members of the family. Lundberg's (Chapter 12) reviewed the advances and remaining problems in the evolution of Ictaluridae (largely exclusive of *Noturus*), including fossil representatives. Also discussed was the morphological and relationships of the family, and species-level problems with both recent and fossil representatives.

Twenty species of Noturus were recognized by LeGrande (1983), who provided a phylogenetic tree based on chromosomal data and morphological characters included in Taylor (1969). To our knowledge this was the first cladistic analysis of a North American freshwater fish group using chromosomal data. Two major clades were demonstrated, one including species of the traditional subgenus Hubbs and one of Schilbeinae plus *Noturus* (sensu stricto). Grady and LeGrande (Chapter 27) combined morphological, karyotypic, and chromosomal characters to elucidate species relationships of Noturus. An innovative series of analyses and character renderings revealed multiple trees and provided insight into variation in homoplasy with differing character types. Proposed relationships were consistent with a monophyletic genus and two subgenera, *Noturus* and *Bubalus;* only some characters provided support for *Schilbeinae* as a monophyletic group.

**Aristidae—Sea Catfishes**

The only freshwater resident of this family in North American waters is *Aristida aquaica* which reaches the southern edge of the Neartic region in the Rio Papaloapan drainage (Miller and Smith, 1986). The widespread *Aristida felis* is also known from the fresh waters of Mexico. Most of the members of this family are found in the basins of rivers. A Wagner parsimony network of DNA fragments in *Aristida felis* revealed a relatively low level of genetic distance among samples from the Atlantic and Gulf slopes (Avise et al., 1987). We are unaware of additional phylogenetic studies inclusive of this genus.

**Pimelodidae—Long Whiskered Catfishes**

Only three species in the genus *Rhina* occur in Neartic fresh waters, and all are known only from the Rio Papaloapan drainage (Miller and Smith, 1986), where a
blind, cave-dwelling species is endemic (Miller, 1984). Skeletal synapomorphies recently discovered by Lundberg and McCleave (1986) placed Rhamdia in a subgroup with five other pimelodid genera. Lundberg et al. (1991) expanded the knowledge of pimelodid relationships in a partly resolved cladogram for the nominal genera of the pimelodid subfamily Rhamdinae, although relationships of Rhamdia were unresolved at the basal node. In an additional paper, Lundberg et al. (1991) provided further resolution of interrelationships of pimelodine catfishes.

Esoxidae—Pikes

Four species of pike, all in the genus Esox, are found in North America; as adults, all are fish eaters and hunt by ambush, darting out to seize their prey from a place of concealment. The northern pike, Esox lucius, and muskelunge, Esox masquinongy, are important sport fishes. Together with the Umbraidae, the Esoxidae forms a monophyletic Esoxace (Lauder and Liem, 1983) and may represent the most primitive extant eelcat clade. The family was considered to be monophyletic by Nelson (1972). Within the family, Esox americanus and E. niger form a monophyletic group sister to a clade inclusive of E. lucius and E. reticulatus, sister to E. masquinongy (Nelson, 1972). According to a tree constructed by Lebeau (1991), the reproductive strategy of E. masquinongy belongs to a common eelcat ancestor, whereas that in E. lucius is derived and unique. Wilson and Williams (Chapter 6) demonstrated the use of the fossil Esox tenuis, together with phylogenetic methods, in establishing ancient habitats of the pikes, their biogeography, and insight into the evolution of their feeding and locomotion behaviors.

Umbraidae—Mudminnows

Three genera and four species of mudminnows are known from North America. The family is of much interest to historical biogeographers because a fifth species in the genus Umbra occurs in Europe; three of the species have relict distributions, and one, Dallia pectoralis, is found only in Alaska and Siberia (see Beringia). In a phylogenetic analysis of the family, Nelson (1972) considered Umbra to be monophyletic, sister to Dallia, and this clade sister to Notemigonus. Within Umbra the two North American species (U. limb, U. pygmaeus) were sister to the European species, U. krameri. Rosen (1974) suggested that the family may not be monophyletic with respect to the Esoxidae, and that relationships among the genera were unresolved. Wilson and Vivier (1982) evaluated phylogenetic relationships within the Umbraidae, and compared their phylogeny with earlier ideas of Cavanese (1959) and the phylogeny of Nelson (1972). Relationships presented by Nelson were preferred in both phylogenetic and compatability analyses. Patterson (1981) accepted this hypothesis of relationships, but also included the fossil taxa Palaeumbra and Umbra. A comparison of phenetic and cladistic approaches to the relationships and classification of eelcat fishes (i.e., Esoxidae and Umbraidae) was discussed in detail by Reif (1987).

Osmeridae—Smelt

This family is represented by six primarily freshwater species in North America. Smelts are circumpolar in cold and temperate coastal waters of the Northern Hemisphere. They are important commercially as food and bait and as an ecological link in the food chain because of their large numbers. Nelson (1970), Rosen (1974), Fink (1984), and others suggested that the family could be paraphyletic with respect to Plecostomus, a genus of the Pacific Coast of Asia. Fink and Weitzman (1982) considered the family to be part of an unresolved monophyletic group also inclusive of Gasterosteidae, Plecostomidae, Retropinnaidae, and Salmonidae. These relationships were also recognized by Rosen (1974), except that Galaxiidae was considered the sister taxon to Salmonidae. Fink (1984) offered two possible phylogenies involving the family. In both resolutions, "Osmeridae" was the sister group to Plecostomus and these two, plus Salmonidae in one cladogram, formed the sister group to other Osmeroidei. Heeke (1984) noted numerous similarities between osmerid larvae and those of Plecostomus. Howes and Sanford (1987) discovered characters demonstrating that Plecostomus was indeed an osmerid and further resolved relationships of some osmerid genera; they found one character indicating monophyly for the family plus Plecostomus.

In an extensive analysis of 84 characters, Beagle (1991) presented a well-corroborated hypothesis of the phylogeny of osmeroid fishes including intrageneric relationships of the Osmeridae. In this study, the Osmerolepis (or Osmeridae) was shown to be a sister to the Galaxiidae (retropterygiidae, Lepidogalaxiidae, Salangidae, Galaxiidae). Wilson and Williams (1991) described a new fossil osmerid genus, Spiraomigonya, from Cretaceous and discussed relationships within the family. Spiraomigonya was shown to form the sister group to Plecostomus; other relationships presented by these authors differed from those of Beagle (1991). Within the genus Osmerus, Lucy et al. (1982) provided a Wagner tree for generic relationships of some populations of O. mordax mordax, O. m. dentex, and O. pellegrinus.

Salmonidae—Trouts, Salmon, and Whitefishes

Seven genera and 44 species constitute the diversity of salmonid fishes in North America. Salmonids are well known for their unique remarkable phenotypic plasticity and many questions regarding species-level taxonomy remain unresolved, especially in the genera Salvelinus and Coregonus. Members of the family are important in the commercial and sport fishing industries of North America and elsewhere. Evidence of monophyly for the family and interrelationships of the genera was presented by Kendal and Behnke (1984). Although the author state that a strict cladistic analysis was not followed. The phylogenetic hypothesis is a synthesis of traditionally informative characters and earlier statements of relationships by Norden (1961), Behnke (1968), Cappel (1970), and Hazel (1982). A PAUP (Phylogenetic Analysis Using Parsimony) analysis of 49 morphological characters and 24 species of salmonids has recently appeared (Smith and Steafer, 1989). These authors also optimized some selected life history traits on their tree and discussed trends in the evolution of salmonid life history. Further, they recommended the use of the name Oncorhynchus for those species that are freshwater adapted; hence, the name for the family remained the same. Smith et al. (1989) reviewed the family and suggested that relationships within the family were complex. They suggested that the family was monophyletic and that the genus Oncorhynchus contained two lineages, one consisting of the anadromous species and the other of the freshwater species. This extensive analysis was based almost entirely on morphological features and included detailed species relationships for Oncorhynchus, Salvelinus, and Coregonus. This analysis was instrumental in evalu-
ing the evolution of the array of reproductive and physiological diversity that characterizes members of the family. More recently, Sanford (1990) substantiated the monophyly of Salmonoidei, but preferred to recognize two sister families, Coregoninae and Salmonidae. Intrafamilies of some genera in the Coregoninae were used by Wilson and Williams (Chapter 6), in conjunction with a phylogeny for the family, to illustrate the use of fossil taxa to test specific character transformations and phylogenies, and to provide insight into the origins of biogeographic patterns and life history features of Recent and extinct species. Relationships of the family to other “salmoniform” groups was discussed by Rosen (1974), Pink and Wetzman (1982), and Pink (1984). Three subfamilies were recognized, in which the Coregoninae was the sister group to a clade including of Salmoninae plus Thymallinae.

Within the family, formal hypotheses of species relationships are increasing rapidly, and most are relying on molecular data bases. A phylogeny of Ocmocychus cherski and its subspecies based largely on diploid chromosome number was shown by Belanek (1988). A strict cladistic analysis was not followed in constructing the tree. Two alternative cladograms based on chromosome number and arm number showed relationships of some species of Salmonina (Cavender, 1984). A largely unresolved cladogram of Salvelinus relationships based on the locations of chromosomal nucleolar organizer regions was presented by Phillips et al. (1989). Both studies demonstrated close relationships among the S. confluentes-salvelinus-alpinus species groups of chars. Grewe et al. (1990) used mtDNA restriction site variation, presented relationships for five species of Salvelinus that were consistent with the above studies. This study provided some evidence for closer affinities between S. alpinus, S. malma, S. fontinalis, and S. namaycush, relative to S. confluentes. Use of nuclear DNA (Phillips and Pyle, 1991) and cytochrome b gene sequences (McVeigh and Davidson, 1991) has further elucidated the relationships of selected salmonid species. A parasimony network of 13 lake trout (Salvelinus namaycush) mtDNA haplotypes was presented by Grewe and Herbst (1988) and modified by Billington and Herbst (1991). Danzmann et al. (1991) included a parasimony network for Ontario brookstocks of Salvelinus fontinalis. Interrelationships of rainbow (Oncorhynchus mykiss), steelhead (O. mykiss, sea-run form), and cutthroat (O. clarki) trout using mtDNA and an unrooted Wagner network showed some detectable divergence among most rainbow and steelhead trout populations analyzed (Wilson et al., 1983). Another mtDNA study of Pacific salmon and rainbow trout (Thomas et al., 1986) demonstrated that the rainbow trout was intimately related to some Pacific salmon. Species of Salmo, Salvelinus, and Ocmocychus were studied by Gyllensten and Wilson (1987) using mtDNA and parasimony analysis. Weishaard et al. (1984) investigated relationships of some “redband” trout (an undescribed complex related to Ocmocychus mykiss) populations employing a phylogenetic perspective; Berg and Fertl (1984) showed Wagner network relationships among brook, brown, and steelhead trout and the chinook salmon; Loudenblager and Call (1980) examined genetic variation in 31 populations of O. clarki and depicted proposed relationships among five subspecies using an unrooted Wagner network; Loudenblager et al. (1986) presented a distance Wagner tree of relationships among native trout from Arizona and New Mexico; Charrutt et al. (1987) presented an unrooted tree of O. niloticus populations using a maximum-likelihood method; Currents et al. (1990) resolved phylogenetic relationships of populations of rainbow trout from several northwestern drainages using allozyme and morphological data; and Bert et al. (1991) revealed genetically distinct sympatric populations of anadromous and non-anadromous Salmo sarrua using an unrooted network connecting mtDNA genotypes from the Gahmu River, Newfoundland.

Using a Wagner parsimony network linking 19 mtDNA clonal lines of Coregonus clupeaformis, Bernatchez and Dodson (1990) showed that two monophyletic assemblages of populations, exhibiting different geographic ranges, exist in Maine and eastern Canada. In a more recent study of mtDNA lineages in 41 populations covering the entire range of C. clupeaformis, Bernatchez and Dodson (1991) identified four (Beringian, Acadian, Atlantic, Mississippi) distinct phylogeographic assemblages as judged from a Wagner parsimony network. In a major study of congregate relationships, Bernatchez et al. (1991) examined 21 taxa using mtDNA restriction analysis. Their data were analyzed both phylogenetically and phylogenetically, resulting in nearly concordant topologies. These major groups were resolved, consisting of (1) species of Prosopium, (2) Stenodus plus five Coregonus taxa, and (3) nine additional Coregonus taxa.

Percopidae—Tout—Perches

The trout-perches, Percopidae, are freshwater inhabitants of medium to large riverine habitats; they are endemic to North America. At least three North American Eocene fossils are known (Patterson, 1981). Patterson (1981) considered the Percopidae to be monophyletic and the sister group to Aphydroleidae plus Amblyopodidae. He further suggested that the ancestor to this family would have inhabited fresh water. Earlier investigations (Rosen, 1962; Rosen and Patterson, 1969) provided evidence for the relationships of these three families and their close affinity to the gilliform fishes. Recently, Rosen (1985) and Patterson and Rosen (1989) noted that the Percopiformes were not monophyletic. No characters were found relating percopids to the monophyletic group of Apheridolidae plus Amblyopodidae.

Aphydroleidae—Pike Perches

The pike perches are represented today by only a single species, Aphydroleus sayanus; it is characteristic of lowland habitats in eastern North America. The fossil record of this family in western drainages was represented by at least three species of Trichophenax (Cuvier, 1826) and Patterson (1981), Rosen (1985), and Patterson and Rosen (1989) considered the family to be monophyletic and sister to the Amblyopodidae.

Amblyopodidae—Carp fishes

The five caviar genera represent a unique element of the fauna. Five species are restricted to the kast regions of eastern United States in spring and cove habitats, and
one occurs on the Atlantic Coastal Plain, all are either blind or have reduced eyes and well developed lateralis systems. Four species are completely troglobitic and have never been captured outside of a cave environment.

The family is monophyletic (Patterson, 1981; Rosen, 1985; Patterson and Rosen, 1989) and the sister to the Apherioideidae. Species relationships within this group warrant additional investigation.

**Lota** — *Cuskfishes*

The only freshwater representative of this largely marine family that occurs in North America is *Lota lota*, a Holartic species. Inter- and intrarelationships of the Gadiformes have been the subject of several recent analyses of morphological data sets (Markle, 1982; Dunn and Mateer, 1984; Rosen, 1985; Dunn, 1989; Howes, 1989; Markle, 1989; Nolf and Stehbunt, 1989; Patterson and Rosen, 1989; Howes, 1990, 1991; Siebert, 1990). Disagreement among these workers exists as to the sister relationships and taxonomic rank of the Gadidae (including *Lotidae*) and many other gadiform groups. Lotidae was recognized to be a distinct family by Dunn (1989), Howes (1989, 1990, 1991), and Markle (1989), but was treated as a subfamily by Markle (1982), Dunn and Mateer (1984), and Nolf and Stehbunt (1989). Howes (1990) placed Lotidae in a monophyletic group along with Pseudidae, Munxaroideidae, Merlucciidae, and Gadidae. Siebert (1990) summarized the character information and relationships relevant to gadiform groups (data from papers in Cohen, 1989) and consistently resolved the Lotidae as the sister group to the Gadidae. Howes (1991) recently recognized Lotidae and part of Pseudidae as sister families. We follow the classification recommended by Markle (1989) and recognize Lotidae as a distinct family; cuskfishes is recommended as a common name.

**Gadidae** — *Codfishes*

The Atlantic tomcod (*Menticirrhus undulatus*) is the only member of the largely marine codfishes that occurs in North American fresh waters. It is found from Labrador to North Carolina (Scott and Scott, 1988) in coastal marine waters and estuaries, but some populations are landlocked (e.g., Lake St. John, Quebec and Deer Lake, Newfoundland) and live out their entire lives in fresh water.

As noted in the above account of the Lotidae, there is some disagreement among recent workers on the sister relationships of the Gadidae (see citations under Lotidae). However, when data from various studies (see citations under Lotidae) were combined, the sister group relationship between the Gadidae and the Lotidae was consistently supported (Siebert, 1990). For an alternative hypothesis of relationships see Howes (1990, 1991). Intragenetic relationships of the Gadidae have not been resolved.

**Gobiesocidae** — *Gobies*

*Gobius flavus* and *G. mexicanus* are the only gobies that occur in North America known to live out their lives in fresh water. Both species occur in streams on the Pacific Slope of Mexico (Briggs and Miller, 1960; Buett and Butch, 1977). The phyloge-
Rivalidae—Rivalines
Two of the three species of *Rivalis* occur in southern México, the third in Florida. *Rivalis marnorotus*, at least in Florida populations, is the only synchronous self-fertilizing hermaphroditic vertebrate known. According to Parenti (1983), *Rivalis* was the pleiomorphic sister genus of all other rivaline genera. A phylogenetic analysis of the family was recently completed by Costa (1990) who provided an alternate hypothesis of generic relationships from those of Parenti (1981); Costa (1991) recently modified his original cladogram.

Profundulidae—Middle American Killifishes
This small family of only five species occurs on both Atlantic and Pacific slopes of Middle America (Miller, 1955). One species, *Profundulus punctatus*, occurs in the Neartic region in southern México. *Profundulus* was the most pleiomorphic clade of the Neartic cyprinodontoid genera (Parenti, 1981). Species relationships are not known.

Fundulidae—Topminnows
The 37 topminnow species of this continent are included in four or five genera; the majority in *Fundulus*. Nearly all of the species are freshwater, are characteristically flattened dorsally, and feed at or near the water's surface. In general, members of this group are colorful, make popular aquarium pets, and some serve as important biological controls of mosquitoes. Until recently, all species of this family were included in the Cyprinodontidae. Parenti (1981), however, determined that not all cyprinodontoids form a natural assemblage. Within Fundulidae, Parenti recognized five genera. *Fundulus* formed the sister group to all other members and *Fundulus* was sister to a clade composed of *Lucania*, *Adinia*, and *Leptocephalus*. Within the latter group, *Lucania* formed the sister group to the other two genera. Wiley (1986b) concurred with some of these conclusions, but placed *Flavobulus* and *Lucania* in an unresolved trichotomy with *Fundulus*. He further noted that *Fundulus*, in its traditional usage, cannot be considered monophyletic. Wiley (1986a) inferred species relationships within *Fundulus* for the subgenera *Fundulus*, *Xenopus*, *Fontinalis*, and *Zygocephalus*. Species relationships within *Xenopus* were presented by Wiley and Mayden (1985), Rogers and Cashner (1987), Cashner et al. (1988), and Grady et al. (1990). The latter two studies focused on allozyme characters and relationships of species and/or populations. Species relationships within *Zygocephalus* and the *Fundulus mystus* species group were in Wiley and Hall (1975) and Wiley (1977). A review of the systematics of *Fundulus* and the impact of molecular methods on resolving genealogical relationships was presented by Cashner et al. (Chapter 13). These authors present species relationships for *Zygocephalus* and *Fundulus*, and argue for combined phylogenetic analyses of multiple data sets, where possible.

The polymorphic *Fundulus heteroclitus*, which occurs along the Atlantic Slope, shows directional changes in gene frequency with latitude. Analysis of mtDNA fragments revealed two major races of the species in a phylogenetic network of clones and populations (Gonzalez-Villaseor and Powers, 1990).

Poeciliidae—Livebearers
At least 75 species of livebearers have been identified as occurring in North American fresh waters. The modification of part of the male anal fin into a copulatory organ, the gonopodium, serves to distinguish poeciliids from the topminnows. Most livebearers are small, rarely exceeding 10 cm in length. As a group they are generally found in warm, fresh, or brackish waters. A number of species are popular in the aquarium trade, and the mosquitofishes (*Gambusia affinis* and *G. holbrooki*) have been introduced widely as mosquito-control agents.

An earlier (Rosen and Bailey, 1964) major monograph on the systematics and biogeography of the Poeciliidae and one on the genus *Xiphophorus* (Rosen, 1960) appeared before the arrival of phylogenetic systematics in North America. Subsequently, Rosen (1979) revised the genera *Heterandria* and *Xiphophorus* and included a detailed cladistic analysis, pertinent remarks about species concepts (including a rejection of subspecies), and expanded on methods in historical biogeography. Rauchenberger et al. (1990) described four new species of *Xiphophorus*, elevated the former *X. montezumae irchmanni* to species status, presented a phylogeny for the monophyletic Rio Pánuco basin swordtails, and analyzed the geography of the nine included species. Parenti (1981) diagnosed the family based on derived characters and recognized three subfamilies. Rauchenberger (1988) offered several area clado-

ograms for a variety of poeciliid taxa in the Caribbean area. A recent systematic treatment of *Gambusia* demonstrated monophyly for the genus; repeated biogeographic patterns between the Pánuco and Guatemalan basins are shown, and some links between Central America and the Greater Antilles are explored (Rasch, 1990). Chapter 17 mapped osteological characters and changes on a tree of the relationships of poeciliid species showing that character changes contain sufficient historical information to recover evolutionary relationships.

Using the Distant-Wagner method, Meffe and Wilcove (1988) examined the genetic relationships of the endangered Sonoran topminnow (*Poeciliopsis occidentalis*). Three natural groupings correspond with geographical domains of the fish. More recently, Meffe and Wilcove (1988) used the same data base to suggest important management practices in the conservation of endangered southwestern fishes, and Echelle et al. (1989) provided a minimum-length network illustrating nearest-neighbor relationships among samples of the Pecos Gambusia (*Gambusia nobilis*).

Goodidae—Splitfins
The live-bearing splitfins of the Mexican *Ptychocheilus* are endemic to the Neartic Realm and include about 46 species in 18 genera. Goodids are one of the most distinctive elements of the central Mexican fish fauna. As a clade they are distinguished from other cyprinodontoids by several features associated with viviparity.
The relationships of goodeids to other cyprinodontiform fishes were obscure until Parenti (1981) discovered derived osteological features shared by goodeids and two oviparous genera in the western United States, Emperichthys and Crenichthys. Both of these genera have been traditionally placed in the Cyprinodontidae, but Parenti expanded the Goodeidae to include them. Miller and Smith (1986) placed both genera in their own family Emperichthyidae, thus limiting the family Goodeidae to include only the Mexican viviparous species. We follow Parenti's (1981) classification here. Interrelationships of the species have yet to be determined.

Cyprinodontidae—Pupfishes

The oviparous pupfishes are typical inhabitants of the deserts of the southwestern United States and northern México. Only about 10 species live outside arid-land regions. Pupfishes can maintain viable populations in highly stressed environments in which other fishes would perish or can adjust rapidly to changed conditions in water chemistry, oxygen, temperature, and food sources. Despite their seeming adaptability to a rapidly changing environment, many local populations have been eliminated and the habitats of a number of pupfishes are threatened. Over 20 Neotenic species of pupfish are now on the list of endangered/threatened/special concern fishes of North America (Williams et al., 1989).

Evidence for the monophyly of this family is presented by Parenti (1981); all Neotenic genera are placed in the tribe Cyprinodontini. This tribe now contains five genera (four of which are freshwater) and 30 species in North America. The genus *Emperichthys* is considered to be marine, but presumably shared a freshwater ancestor with *Crenichthys*. Relationships developed by Parenti (1981) for these genera consist of two monophyletic sister groups, one containing unresolved relationships between *Cyprinodon*, *Megapijula*, and *Jordanella*, and the other including the sister genera *Florichthys* and *Crenichthys*. Parenti also discussed the potential for *Cyprinodon* and *Jordanella*, or some *Cyprinodon* and *Jordanella* as a monophyletic group. Relationships within the diverse genus *Cyprinodon* are largely unresolved. In the first available phylogeny for members of this genus Echelle and Echelle (Chapter 35) compared allozyme variation in the *C. variegatus*, *C. eximius*, and *C. macularius* species groups with *C. elegans*, *Jordanella*, and *Florichthys*. These authors also examined species and population relationships in the *variegatus* group and hypothesized the evolution of Island species from the widespread and distant ancestral species, *C. variegatus*.

Hemiramphidae—Halfbeaks

This family contains 12 genera and at least 80 species (Parin et al., 1980). *Hyporhamphus*, the most species rich genus in the family, contains 34 species, some of which are marine, some estuarine, and some fresh water (Collette et al., 1984). Only one hemiramphid species, the California halfbeak, *Hyporhamphus brasiliensis*, occurs in the fresh waters of North America. The species is found in coastal streams from southern California to at least the Sonoran-Sinaloan coastal area of Mexico. In his original description of *Hyporhamphus patrus* (a synonym of *H. roseus*), Miller (1945) reported a ripe male and female from the Rio del Fuerte. We assume the species spawns in fresh water.

Hemiramphidae is the sister family of the flying fishes, Exocoetidae (Collette et al., 1984). Cladistic relationships of the genera and species of halfbeaks have not been resolved.

Belonidae—Needlefishes

Members of this family have a circumtropical distribution and may be either marine, estuarine, or freshwater in habitats. One species, *Strongylura hubbii*, occurs regularly within freshwater habitats in southern México; *S. marina* is found over 370 river kilometers inland from Atlantic and Gulf coastal waters (Boschung, 1989; Pierson et al., 1989). Some populations of *S. marina* clearly spawn in fresh water.

Evidence for monophyly of the family and a sister group relationship with the Scromberesocidae were presented by Collette et al. (1984). These authors further noted that the freshwater genera *Pseudotomus*, *Pomatogobius*, and *Belonias* were probably all derivatives of the genus *Strongylura* or its ancestor, potentially rendering this genus paraphyletic. A more recent analysis of relationships within the family by Broughton et al. (1991) revealed that *Strongylura* is, in fact, paraphyletic with respect to *Pseudotomus*, *Aleiodes*, *Tylurus*, *Xenomystus*, *Pomatomus*, and *Belonias*. In this study *S. marina* formed a basal sister group within this clade (exclusive of *S. colias*) and *S. hubbii* formed an unresolved trichotomy with *Pseudotomus*, other *Strongylura*, and some other genera.

Gasterosteidae—Sticklebacks

This family is famous for the numerous studies of its species by ethologists and physiologists. The mating and nest building of sticklebacks have attracted much attention for many years. At least six species in four genera are found in North American fresh waters. The recognition of only six species, however, falls to account for the tremendous genetic diversity seen, particularly in the *Gasterosteus aculeatus* and *Pungitius pungitius* complexes (see Haglund et al., 1984). Interrelationships of species within the order Gasterosteiformes were treated by Pietsch (1978).

McLennan et al. (1988) provided a phylogenetic analysis of gasterosteid genera using only behavioral characters with the *Ambloplitidae* (tube-snout) as the outgroup. Members of the ingroup and outgroup are the only fishes known with a kidney-produced substance that is used by males to glue plant material into a nest. Using 27 behavioral characters McLennan et al. demonstrated that *Pungitius* plus *Colias* are sister to *Gasterosteus*, that *Apeltes* is the sister to the aforementioned genera, and that *Spinachia* (the fifteen spine stickleback of northern Europe) is the plesiomorphic sister taxon of the family. An earlier (Hudon and Guderley, 1984) allozyme analysis of four gasterosteid genera placed *Pungitius* as the sister to *Gasterosteus*, and *Apeltes* sister to *Pungitius* plus *Gasterosteus*. Haglund et al. (Chapter 14) examined genetic variation in the polymorphic *P. pungitius* species complex, representing Asia, Europe, and North America.

Syngnathidae—Pipefishes and Seahorses

Only three pipefish species (*Microphis brasiliensis*, *Pseudophallus starki*, *Syngnathus acodii*) are included here, and are all coastal in distribution. Members of the family
are mostly marine or estuarine in habitat; all of the species are characterized by an elongate, plated body form. Relationships of these species to other members of the family have not been documented. The phylogenetic relationships of gasterosteiform families were reviewed by Pethybridge (1978) and Fritzsch (1984). The family is considered monophyletic and closely related to the family Solegnostomidae.

Moronidae—Temperate Basses

Four species of temperate basses, *Morone*, are native to North America. Members of this family are popular in the sport fishery and typically inhabit lakes, reservoirs, and medium to large rivers. The four species form a monophyletic group and were removed from the family Percichthyidae by Johnson (1984) based on a lack of evidence for common ancestry with this family and any other percoid group. Some affinity with the Centropomidae was suggested by Johnson in light of synapomorphies shared between these two families. Relationships among the four species of temperate basses are unknown. Jenkins (1988) suggested the common name "striped basses" for this newly recognized family, but too few of the species are actually striped. Until a more appropriate name is suggested, we continue to use the common name established for the Percichthyidae.

Centrarchidae—Sunfishes

Among the most sought-after sport fishes in the world are the sunfishes and basses, a group of 32 species in nine genera endemic to North America. Their native range is presently east of the Continental Divide except for *Acanthepsis interrupta*, the only extant centrarchid native west of the Rocky Mountains; several fossil sunfishes are known from western North America (Cavender, 1980). A number of species, particularly the largemouth bass and bluegill, have been widely introduced throughout the world. The aggressive and pugnacious behavior of male sunfish has interested many investigators and continues to fascinate students of animal behavior and natural history. Members of *Lepomis* show a considerable propensity to hybridize in nature.

In one of the earlier applications of Wagner methods to genetic distance data, Avis and Smith (1977) produced a tree of seven centrarchid genera. In this analysis *Pomoxis* was the sister to *Lepomis* plus *Micropterus*. The genus *Elassoma* (formerly placed in the Centrarchidae) was placed as the sister group to all other centrarchids. A similar approach using Prevosti genetic distances and Wagner methods for 12 species was given by Parker et al. (1985). Mok (1983) provided a phylogenetic hypothesis for centrarchid genera using only kidney characters but with little resolution. In a novel approach, Lauder (1986) used ecological, behavioral, functional, and morphological features to construct a tree of five species of *Lepomis* and most centrarchid genera; a number of trichotomies resulted. Mitochondrial DNA of southern populations of three species of *Lepomis* were analyzed using a Wagner network by Birmingham and Avis (1986). A phylogeny of all centrarchid genera based on superspacial and predorsal bones was presented by Mabee (1988), showing *Micropterus* as the sister taxon to remaining members of the family, *Lepomis* as sister to *Emys canthus*, and *Centrarchus* sister to *Archoplites*. A similar but more detailed phylogeny of all species was given in Wainwright and Lauder (Chapter 16), based on unpublished data by Humphries and Lauder and used to explore the evolution of feeding behavior in these fishes. Klassen and Beverley Burton (1988) included a Wagner tree of 11 centrarchid species in an analysis of host-parasite coevolution based on centrarchid data from Avis and Smith (1977) and Mabee (pers. comm.). Observations of the ontogenies of 58 characters and the construction of five different trees of centrarchid relationships led Mabee (1989) to conclude that the ontogenetic criterion was generally invalid as a polarity criterion for phylogenetic systematics.

Elassomatidae—Pygmy Sunfishes

Pygmy sunfishes are common inhabitants of heavily vegetated, lowland waters in eastern North America. The six species are small, reaching a maximum length of about 40 mm. This family was removed from the Centrarchidae by Branson and Moore (1962) on the basis of morphological and behavioral distinctiveness. This decision was recently supported by Johnson (1984) in an analysis of Perciform. At present there is no evidence that the family is monophyletic or that it is closely related to any of the percoid or poutiform groups (Johnson, 1984).

Percidae—Perches and Darters

Fishes of the family Percidae include some of the most colorful and popular native fishes of North America. The family is the second largest with 165 species in five genera. All of the North American species, except those of *Percina* and *Stizostedion*, are collectively referred to as darters; *Etheostoma* represents the most diverse genus for the continent. Significant contributions exist detailing the diversity within this family, but additional systematic and evolutionary research with percids is needed. Reproductive behaviors are quite varied for the group, from unspatIALIZED distribution of eggs over the substrate to complex clustering or clumping of eggs on the underside of rocks (Pate, 1985). Species of *Stizostedion* and *Percina* are popular sport fishes; they typically inhabit large rivers and lakes, while darters are most diverse in small rivers and creeks.

Monophyly of the family was substantiated by Johnson (1984) and Wiley (Chapter 7), but some previous superspecific groupings within the family may be unjustified. Wiley (Chapter 7) presented phylogenetic relationships of all known genera, except *Perca*, which forms the sister group to all other genera. Both *Percina* and *Stizostedion* were considered monophyletic, although few studies have examined species relationships. Billington et al. (1999) compared proteins and mtDNA divergence and relationships of the two North American species of *Stizostedion* and the European *S. luciopeus*. A restricted maximum likelihood analysis of 15 populations of *Stizostedion vitreum* was presented by Ward et al. (1989) who showed significant genetic divergences between Great Lakes and more northern populations. The darter
genera number three and comprise a monophyletic assemblage with *Crystallaria* (formerly *Ammonocypris*, see Simons, 1991) forming the sister group to *Percina* and *Etheostoma*. Other members of the former genus *Ammonocypris* form a monophyletic group and a subgenus of *Etheostoma* (Simons, Chapter 8). The darter clade was sister to the European genus *Romancichla* (Willey, Chapter 7).

The most complete evaluation of relationships among the darters was presented by Page (1981). This analysis was the first attempt at determining ancestor-descendant relationships among all known species and genera, and was based upon a Wagner analysis of morphological characters. More recently, Page (1985) hypothesized additional species relationships for the *Etheostoma* subgenus *Ozarka*, *Notemigonus*, *Catonius*, *Bolosoma*, *Gammacara*, *Nauvanna*, and *Etheostoma* based on morphological, color, and behavioral traits. Paine (1990) used some of Page's (1985) phylogenies to help explain some darter life history tactics. Simons (Chapter 8) presented alternative relationships for *Gammacara*, *Bolosoma*, *Nauvanna*, and *Etheostoma* based on morphological data; these relationships were used by Johnston (1989) in a discussion of the evolution of reproductive behaviors of some darters. Page and Bart (1989) examined the evolution of egg-mimicking structures within the subgenus *Catonius* and *Bolosoma*. Bart and Page (Chapter 20) used the published relationships of Page (1981, 1985) to partition out historical influences on life history parameters of percididae.

Phylogenies have also been presented for other individual subgenera of *Etheostoma* and *Percina*. Burr (1978) and B. (1980) offered hypotheses for relationships within the subgenus *Micropterus*. Willey and Mayden (1985) summarized relationships for species of the subgenus *Ammonocypris* (*Etheostoma*) and species of the *E. variabilis* species group, along with the subgenus *Hedapleurus* and *Swainia* of *Percina*. Wolfe et al. (1979), Mayden (1985a), and Braasch and Mayden (1985) proposed relationships within the subgenus *Catoma* of *Etheostoma*. Species relationships within *Ozarka* of *Etheostoma* and *Swainia* of *Percina* were examined by Mayden (1985b, 1987b). Phylogenies of the E. *variabilis* complex were shown in McKaen et al. (1984) and Mayden (1987a, b). Bailey and Eiler (1988) hypothesized relationships for species of the subgenera *Libicara*, *Etheostoma*, and *Etheostoma* in *Etheostoma*, and commented on relationships of other darter groups. A phylogeny of species of the subgenus *Notemigonus*, as judged from a suite of 17 external morphological characters, was presented by endangered (1989). Species relationships proposed by these authors were employed by Brodie et al. (1992) to illustrate the predictive potential of phylogenetic trees and their use in conservation biology.

**Cichlidae—Cichlids**

At least 14 species of cichlids are known from the Neotropical region and all are presently placed in the New World genus *Cichlasoma*. Cichlids are well known for their complex and fascinating breeding behaviors and for the frequent occurrence of territorial and color polymorphisms.

On the basis of four apomorphic characters, Stassev (1981) proposed that the Cichlidae, as presently recognized, is monophyletic. The family is sister to the Embioptocidae (surgeperches) plus Labridae (wrasses) (Lauder and Liem, 1983), but Stassev and Jensen (1987) found the Cichlidae sister to a clade inclusive of the Embioptocidae, Pomacentridae, and Labridae. Phylogenetic relationships of Neotropical cichlid genera and species are being actively explored, and some distinct groups within *Cichlasoma* are recognized. Stassev (1996, 1991) summarized previously proposed phylogenetic hypotheses of major groupings within the Cichlidae. Neotropical cichlid genera were argued to form a monophyletic group, sister to some African genera, but three alternative schemes of relationships among the New World genera were proposed. "Cichlasominae" were composed of two clades and were found to be either sister to "Geophagines" or part of an unresolved monophyletic group inclusive of *Cichla*, "Crenicichilines," and "Geophagines."

The phylogeny of key South American cichlid genera is only beginning to be unraveled (Stassev, 1982, 1987). Kullander (1983) recently restricted the name *Cichlasoma* to South American species, indicating that cichlids in the Neotropical region will eventually be classified in other genera.

**Embioptocidae—Surgeperches**

This largely marine family of live-bearing fishes includes only one freshwater species, *Hystromacrus brasili*, which occurs exclusively in California. The Embioptocidae are sister to the Labridae (wrasses) (Lauder and Liem, 1983). Although no formal cladistic analysis is available for the genera and species of surgeperches, members of the family were the subject of a cladistic exercise in a recently published ichthyology laboratory manual (Caillet et al., 1986).

**Mugilidae—Mulletts**

Three genera and four species of mullet occur in North American fresh waters. *Agonostomus monticola* may be catadromous (Gilbert, 1978) and the other three species are known freshwater streams for considerable distances.

The family Mugilidae is presumed to be closely related to the Syngnathidae (barracudas) and Polydentidae (breezes) (de urgency, 1984). In a recent review of the cichlid pharyngobranchial organ and its phylogenetic significance, Harrison and Howes (1991) concluded that *Agonostomus and Johnius* were near the base of the cichlid tree and that *Mugil* was placed in a polytomy with several other genera near the top of the tree.
Electroidae—Sleppers

Only seven species of North American sleepers, in the genera Dromichthyis, Eleginis, and Gobiosoma, have populations regularly inhabiting fresh water where they are presumably carrying out their life cycles (see Miller and Smith, 1986; F. L. Pezold, pers. comm.). While no cladistic hypotheses of the generic or specific relationships of electroids have been published, some of the genera presently included in the family are apparently more closely related to gobids (Hoese, 1984), thus rendering the Electroidae paraphyletic.

Gobiidae—Gobies

Gobies are generally inhabitants of coastal marine and estuarine habitats; however, seven species regularly inhabit freshwater habitats in North America where they are presumably carrying out their life cycles. The tidal goby, Eucyclogobius newberryi, an inhabitant of the Pacific coastal streams of California, has populations capable of completing all or nearly all of their life cycle in fresh water (Moyle, 1976; Swift et al., 1989). Two gobies of the genus Macrhybosis inhabit the fresh waters of central and southern Mexico. Two species of the genus Awaous, one species of Chromogobius, and one species of Gobionellus have been recorded from pure fresh water in several coastal rivers of North America (F. L. Pezold, pers. comm.); species of Awaous are known to spawn in fresh water. Phylogenetic relationships of most gobies are unresolved (Springer, 1983; Hoese, 1984; Birdsong et al., 1988), however, Parenti (1991) included a partially resolved tree of the relationships of sculpine genera and an area cladogram of ocean basins wherein the genera are found. From her study she concluded that "a continent is part of the biogeographic regions of all the oceans it contacts."

Cottidae—Sculpins

Members of this family are primarily marine or euryhaline. Two genera of freshwater sculpins occur in North America: Cottus with 23 named species and Myoxocephalus with two species. As a group, North American sculpins are generally found in cold lakes or fast-flowing streams where they are known to be efficient benthic predators. In a preliminary hypothesis of cottid relationships, Myoxocephalus and Cottus formed part of an unresolved polyphyly with several other sculpin groups (Washington et al., 1984). The two genera are apparently monophyletic. In Yabes (1985) analysis of cottid relationships Cottus occurred near the base of the cottid tree and Myoxocephalus had unresolved relationships with respect to several other genera. Yabes (1991) considered the Myoxocephalus group sister to the Aleutian Islands sculpin Bolitogobius myxolepis plus the Atherinidae group. Analyses of species relationships among Cottus and Myoxocephalus are not yet available.

Synbranchidae—Swamp Eels

The only species of swamp eel in North America is Ophiobatis australis.
getting the English translation of Hennig's *Phylogenetic Systematics* published in 1966. In the 20 or so years since phylogenetic theory was brought to the attention of North American ichthyologists, a genuine revolution in systematics and biogeography has occurred. Prior to this period, ichthyologists and other systematic biologists were operating under a different, largely descriptive, systematic methodology.

To our knowledge, the first three papers that included Neartic fishes and used the phylogenetic approach were published in 1969. One was by Nelson (1969a) on Ostegostrumorph fishes (including the North American Hiodontidae); another was by Nelson (1969a) on Gill arches and vertebrae classification (including a tree of relationships of sturgeons, paddlefishes, gars, and bowfins); and a third was by Rosen and Patterson (1969) on paracanthopterygian fishes (including remarks on the relationships of North American percopiform fishes). Shortly thereafter, Smith and Koehn (1971) produced the first Wagner network for a Neartic fish group (western catostomids). Since these early papers, the phylogenetic approach has been used in the orthodox sense to elucidate relationships of many groups. In fact, through 1990, there have been at least 180 published papers applying phylogenetic methodology to systematic problems among our native fishes (Fig. 2). Nearly 100 of these papers have used morphological data sets in their analyses and the remainder have combined morphological, behavioral, and/or genetic (i.e., mtDNA, NRS, karyology, allozymes) data sets or have relied strictly on genetic data sets. In some 26 families (Petromyzontidae, Actinopterygii, Anguillidae, Elopidae, Characidae, Atherinidae, Pimelodidae, Amblyopiniidae, Loricariidae, Rutilidae, Prophyridiidae, Goodeidae, Cypriomodontidae, Belonidae, Hemirhamphidae, Syngnathidae, Moconidae, Elassomatidae, Cichlidae, Embiotocidae, Mugilidae, Eleotridae, Curiridae, Pleuropterygidae, Soleidae) phylogenetic relationships of genera or species are unresolved or largely unknown (Table 4). Phylogenetic hypotheses are available, however, for some genera or species groups in about half of the 50 families known from North American fresh waters. These generalizations have been the foundation for further studies on the origins of communities, the evolution of behaviors, modes of speciation, conservation genetics, patterns in historical biogeography, character evolution, and other fields of comparative biology.

Our review of the North American freshwater fish fauna reveals two general observations: 1) the fauna is distinctive with 128 endemic genera and eight endemic families, contains groups with diverse ecological strategies, and imparts many distinctive distributional patterns; and 2) our existing knowledge of the phylogenetic relationships among species is steadily increasing but still inadequate, especially concerning the overall diversity and the many years of effort directed toward understanding the fauna. It is impossible, however, to ignore the fact that many of our advances have been dependent upon an existing data base revealing the diversity and distributions of these fishes constructed without the benefit of ancestor-descendant hypotheses for species or the theory of phylogenetic systematics. Thus, we are indebted to our academic ancestors and present-day colleagues for expounding on the evolutionary hypotheses presented in this chapter.

Future progress in unraveling the evolution of North American fishes will include

### Table 4
North American Freshwater Fish Families in which Phylogenetic Relationships of Genera or Species are Unresolved or Largely Unresolved

<table>
<thead>
<tr>
<th>Family</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percomyzontidae</td>
<td>14</td>
</tr>
<tr>
<td>Acanthistidae</td>
<td>15</td>
</tr>
<tr>
<td>Anguillidae</td>
<td>16</td>
</tr>
<tr>
<td>Elopidae</td>
<td>17</td>
</tr>
<tr>
<td>Characididae</td>
<td>18</td>
</tr>
<tr>
<td>Atherinidae</td>
<td>19</td>
</tr>
<tr>
<td>Pimelodidae</td>
<td>20</td>
</tr>
<tr>
<td>Amblyopiniidae</td>
<td>21</td>
</tr>
<tr>
<td>Mugilidae</td>
<td>22</td>
</tr>
<tr>
<td>Atherinidae</td>
<td>23</td>
</tr>
<tr>
<td>Rutilidae</td>
<td>24</td>
</tr>
<tr>
<td>Cichlidae</td>
<td>25</td>
</tr>
<tr>
<td>Pleuropterygidae</td>
<td>26</td>
</tr>
</tbody>
</table>

the continued interest in the development of phylogenetic hypotheses for genera and species. The diversity of our native fish fauna will allow for future investigations in which novel theories concerning ecological and evolutionary processes may be developed and tested. The limiting resource in this equation, however, has been and will continue to be for some time the development of a phylogenetic data base for the future.

An extensive literature on the North American fish fauna and other organisms seeks explanations to questions of an historical nature. Likewise, many hypotheses have been advocated with regard to the temporal evolution of faunas and communities as well as the ecological, morphological, behavioral, and genetic traits displayed by the individual species. As advocated by Brooks (1985), Mayden (1987a, b, Chapters 1 and 30), and Brooks and McMellon (1991, Chapter 3), questions such as these are most effectively addressed only when knowledge of the geological histories of the taxa are available.

Direct estimates of many historically pertinent questions have only recently become a reality for the North American fish fauna. Synthesis of previously developed information, together with recent phylogenetic hypotheses of species, has resulted in initial evaluations of modes of speciation by Wiley and Mayden (1985). Aside from the numerous applications throughout this volume, these phylogenetic hypotheses have been instrumental in examining the origins of communities (Mayden 1987a, 1988b, Nelson and Ladiges, 1991, certain species associations (Mayden 1987a), and the evolution of behaviors (Page, 1985; McMellon et al., 1988; Page and Bart, 1989; Page and Johnston, 1990; Matsuaki et al., 1991) and life history parameters (Page, 1985; Smith and Stealey, 1989; Patim, 1990). Insightful advances in historical biogeography of the fish fauna and new methods in biogeography have recently been advanced through the use of genetic and molecular data by Rosen (1979), Wiley and Mayden (1985), Mayden (1985b, 1987a, b, 1988b), Minckley et al. (1986), and Nelson and Weigelt (1993). Likewise, these data have contributed to our understanding of character evolution, ontogeny, and complex morphologies, as evidenced by contributions in Osse et al. (1984) and Bookstein et al. (1985), and investigations by Page (1985), Mabe (1986), Lauth (1982, 1986), Strauss (1990), and Boughton et al. (1991). Innovative ideas in the areas of conservation genetics,

---

**Table 4. North American freshwater fish families in which phylogenetic relationships of genera or species are unresolved or largely unresolved.**

<table>
<thead>
<tr>
<th>Family</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percomyzontidae</td>
<td>14</td>
</tr>
<tr>
<td>Acanthistidae</td>
<td>15</td>
</tr>
<tr>
<td>Anguillidae</td>
<td>16</td>
</tr>
<tr>
<td>Elopidae</td>
<td>17</td>
</tr>
<tr>
<td>Characididae</td>
<td>18</td>
</tr>
<tr>
<td>Atherinidae</td>
<td>19</td>
</tr>
<tr>
<td>Pimelodidae</td>
<td>20</td>
</tr>
<tr>
<td>Amblyopiniidae</td>
<td>21</td>
</tr>
<tr>
<td>Mugilidae</td>
<td>22</td>
</tr>
<tr>
<td>Atherinidae</td>
<td>23</td>
</tr>
<tr>
<td>Rutilidae</td>
<td>24</td>
</tr>
<tr>
<td>Cichlidae</td>
<td>25</td>
</tr>
<tr>
<td>Pleuropterygidae</td>
<td>26</td>
</tr>
</tbody>
</table>
management of endangered species, and phylogenetics in conservation biology have also been possible with appropriate historical approaches to data analysis (Vijeshhoek et al., 1985; Brooks et al., 1992). Finally, estimates of rates of speciation and comparisons among groups with respect to gradual or punctuated modes attempted earlier by Avise (1977) and others can only be evaluated in light of their individual phylogenies (Mayden, 1986, Chapter 30; Gold et al., Chapter 19).

**SUMMARY**

The two major objectives of this contribution were to briefly review the composition of the recent native North American fish fauna and to provide a synopsis of what is known of the phylogenetic relationships of the species. At least 1,061 species placed in 196 genera and 50 families have been recorded from inland waters. About 966 species, 128 genera, and 8 families are endemic to the Neartic realm. The six dominant fish families include Cyprinidae (with 302 species), Percidae (165 species), Poeciliidae (75 species), Catostomidae (70 species), Ictaluridae (48 species), and Goodeidae (46 species). North American fresh waters were divided into 15 distinctive provinces on the basis of environment, geography, history, and uniqueness of the fish fauna. For each province, the number of native families and species is given. We did not include number of genera because of impending changes in several large families (e.g., Cyprinidae, Catostomidae, Goodeidae). Within the 15 fish provinces are many drainages or regions of significant endemism, for example, the Mobile basin (about 40 endemic species), the Tennessee River drainage (30 species), the Rio Pánuco drainage (29 species), the Cuizzato River drainage (22 species), the Rio Lerma-Santiago drainage (17 species), the Ozark Uplands (16 species), the Columbia River basin (13 species), the Sacramento-San Joaquin River drainage (12 species), the Cumberland River drainage (9 species), and the Roanoke-James River drainage (8 species).

The application of phylogenetic methods to the Neartic fish fauna has only taken place recently, beginning in 1969. Since that time about 180 published papers using this approach have appeared (Fig. 2). The relatively uniform acceptance of phylogenetics in recent years has resulted in a significant increase in the number of papers relying on Hennig's method. An average of about 14 papers using phylogenetics have been published each year between 1981 and 1990, whereas an average of three papers was published each year from 1969 to 1980. In over two-thirds of these papers morphological data bases have served in identifying sister group relationships; the remaining papers have relied largely on genetic or behavioral data. For some 26 families phylogenetic relationships of genera and species are unresolved or largely unresolved.

Some of the more novel uses of phylogenetics include Leaude's (1983) analysis of functional morphology of feeding in sunfishes, the hypothesis for the origin of an all-female species of silverside by Schelte et al. (1983), Pagen's (1985) evaluation of the evolution of reproductive behaviors in darters, Mabes's (1988) review of sunfish relationships using ontogenetic characters, McLennan et al.'s (1988) analysis of stickleback relationships based strictly on behavioral traits, and Mayden's (1988b) biogeographic analysis in which drainages are treated as evolutionary units and fishes as characters. It is clear from our synopsis of the phylogenetic relationships of Neartic freshwater fishes that phylogenetic hypotheses already generated have not gone unused. In fact, they have been the foundation for further research in several areas of historical ecology. It is our conclusion that the continued support and development of phylogenetics for North American freshwater fishes is highly desirable and will serve as important insights into evolutionary biology as a whole. Further, it is clear that historical questions in comparative biology can most effectively be addressed only when knowledge of the geological histories of the taxa are available.

**LITERATURE CITED**


