Centrarchid Fishes
Diversity, Biology, and Conservation

Edited by
S. J. Cooke and D. P. Philipp
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S. J. Cooke and D. P. Philipp

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*B. D. Neff and R. Knapp*

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*D. D. Aday, J. J. Parkos III, and D. H. Wahl*

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Preface

The fishes in the family Centrarchidae are more commonly known as the freshwater sunfishes, a warmwater clade with 34 extant species that are endemic to North America. This group of warmwater fishes generally consists of small to moderately sized individuals that are highly colored (like the bluegill on the cover of the book). The sunfish family includes such prominent sportfish species as the largemouth bass, Florida bass, smallmouth bass, and bluegill. The largemouth bass is the most popular recreational sportfish in North America and is the basis for a large industry. In addition, bass are the frequent quarry of anglers participating in competitive angling events. Centrarchid fishes also play important ecological roles in structuring communities. They are commonly the dominant top-level predators in the diverse lentic and lotic warmwater communities of freshwater fishes in eastern North America. They provide forage for many other species and also serve as hosts for sensitive life-stages of threatened bivalves. The reproductive strategies of centrarchid fishes are especially interesting in that the male fish provide sole parental care for offspring over periods ranging from maybe as short as 1 or 2 days (for Sacramento perch) to 4 to 5 weeks (for smallmouth bass). In addition, centrarchids have been widely introduced around the globe, leading to a number of conservation concerns.

Due to the popularity of this group of fishes, state and provincial fisheries managers devote substantial efforts toward managing these species. Some regions place significant emphasis on stock enhancement using cultured fish. Although there has been a recent explosion of research on sunfish species in response to their abundance and importance, at present, this large body of literature is not supported by any comprehensive syntheses on the biology and ecology of these fishes. As managers and scientists press forward with research, management, and conservation strategies, there will be an increased need to coalesce the disparate accounts of sunfish biology. Indeed, an understanding of their physiology and behavior is essential for understanding the magnitude of the threats faced by these fishes. The tome that we have developed with our team of expert authors represents a synthesis of the current state of knowledge on sunfish biology. An overriding goal of the book is to celebrate the life-history variation evident in this group of fishes (hence the use of the word “diversity” in the title of the book). A secondary objective was to summarize the linkages between basic ecology and the applied management and conservation of centrarchid fishes.

Contributors were asked both to synthesize the existing literature and to contribute novel data from unpublished or forthcoming works. For that reason, we developed a team of contributors that represent those individuals at the cutting edge of centrarchid research. Authors were asked to provide coverage of all species, not just those of economic importance. Almost every author, however, identified that the majority of the available data and research were focused on several species (largemouth bass, smallmouth bass, bluegill, pumpkinseed, rock bass, black crappie, and white crappie). Detailed species accounts (of 33 of the 34 extant species; excludes the Alabama bass, Micropterus henshalli) and a key to the centrarchids were developed by M. Warren and can be found at the end of the book. In total, the book contains 13 chapters that cover almost all aspects of sunfish biology and management. One notable omission from the list of chapters is the one focused on the reproductive biology of the centrarchid fishes. This is intentional because various aspects of reproduction were included in all of the chapters (e.g., hybridization, early life history, population biology, energetics, culture) and are thus covered throughout the book. Alternative reproductive tactics are covered independently. The detailed species accounts at the end of the book also include summaries of reproductive biology for all of the centrarchid fishes. We are particularly excited to include a chapter on winter biology, a topic of high importance to centrarchid fishes (i.e. overwinter mortality can influence recruitment), particularly toward the northern edge of their range. To our knowledge, there are no other “taxon” specific tomes that include coverage of winter biology. Thanks to the talented authors and the many referees, we are confident that this book is THE stand-alone reference on the biology of one of the most important groups of fishes in North America.

Emphasizing the diversity of centrarchid fishes and the ongoing research efforts to clarify phylogenetic relationships, during the period when the book was being typeset an additional centrarchid was elevated to the species level. That addition is Micropterus henshalli (Hubbs and Bailey 1940), the Alabama Bass (See Baker, W. H., C. E. Johnston, and
G. W. Folkerts, 2008. The Alabama Bass, *Micropterus henshalli* (Teleostei: Centrarchidae), from the Mobile River basin. Zootaxa 1861:57–67). The previously recognized subspecies of *Micropterus punctulatus* from the Mobile River system of Alabama, Georgia, and Mississippi has been elevated to species status on the basis of morphological evidence, but it had long been recognized as distinct according to ecological, morphometric/meristic, and genetic characters. As such, although we formally recognize 34 extant centrarchid species, only 33 of them are covered extensively in this book. We do not include a formal natural history account for *Micropterus henshalli*, however, details can be found under the account for *Micropterus punctulatus* where it is described as a subspecies. We were able to make some limited changes at the proof stage to Chapter 1 in recognition of this taxonomic change, however, the phylogenies presented exclude this species. Given the many advances in molecular genetics and taxonomy, we would expect that the number of centrarchid fish species would increase in the coming years. Hence, although an inconvenience to those of us working on this book project, this taxonomic elevation is further evidence of the diversity of centrarchid fishes.

We thank the many individuals that contributed to the book either intellectually or in the form of other support. This project was initiated when Cooke was an NSERC and Killam Post-Doctoral Fellow in the Centre for Applied Conservation Research at the University of British Columbia. At the time, Cooke was mentored by Dr. S. Hinch and Dr. T. Farrell, both of whom provided the freedom and encouragement to pursue this project. In the final phases of editing, Cooke was supported by the Natural Sciences and Engineering Research Council of Canada, the Rainy Lake Fisheries Charity Trust, the Ontario Ministry of Research and Innovation (Early Researcher Award), and Carleton University. D. Philipp was supported by the Illinois Natural History Survey and the Illinois Department of Natural Resources.

We recognize and appreciate tremendously that the Queen’s University Biological Station provided a stimulating, productive, and fun environment to launch the idea for the book. We are particularly indebted to A. Weckworth and L. Thompson who completed detailed technical editing to ensure consistency in format and style throughout the book. D. Ramesh, Project Manager from Laserwords Private Limited in India, provided additional technical editing and facilitated the typesetting and proof changes during the final phases of the publication process. We also thank our families for continued support and acceptance of our crazy field schedules. From Blackwell Science Publishers (UK), N. Balmforth, L. Price, and K. Nuttall provided support and continual encouragement throughout the protracted writing and editing process. We also wish to acknowledge all of the authors for providing contributions that were of high quality and incredibly comprehensive. The project took several years to complete, and our authors were extremely patient. Furthermore, we thank the many anonymous (unless declared and listed in the acknowledgments) referees for providing thoughtful reviews of the lengthy chapters.

*S. J. Cooke and D. P. Philipp, Eleuthera, The Bahamas, December 2, 2007*
About the Editors

S. J. Cooke: Cooke received his undergraduate and M.Sc. degrees from the University of Waterloo. He completed his Ph.D. research at the University of Illinois in 2002 while working with Dr. D. P. Philipp and Dr. D. H. Wahl at the Illinois Natural History Survey. Cooke was then awarded an NSERC Post Doctoral Fellowship and Izaak Walton Killam Fellowship, which he held as a postdoctoral fellow at the University of British Columbia where he worked with Dr. S. Hinch and Dr. T. Farrell. In 2005, Cooke became an Assistant Professor in Environmental Science and Biology at Carleton University (Ottawa, Canada) where he is Director of the Fish Ecology and Conservation Physiology Laboratory. Cooke, his students, and collaborators, study how fish respond to natural and anthropogenic stressors and how individuals, populations, and species vary in their response. Cooke has published over 100 peer reviewed papers, about half on fish in the sunfish family covering topics such as the energetics of parental care, the physiological consequences of angling practices, and the consequences of outbreeding on fish performance. Cooke has been the recipient of the American Fisheries Society Award of Excellence in Fisheries Management and an Early Researcher Award from the Ontario Ministry of Innovation. He is also an editor for the journal Endangered Species Research and is on the Editorial Board for Fisheries Research. Cooke is an Affiliate Scientist with the Illinois Natural History Survey, Adjunct Professor at Queen’s University, and an Honorary Research Associate at the University of British Columbia. He and his wife currently reside in Ottawa, a region rich with centrarchid dominated fisheries.

D. P. Philipp: Philipp received his undergraduate degree from Lafayette College and his Ph.D. from the University of Massachusetts in 1976. He is currently Principal Scientist at the Illinois Natural History Survey (INHS) and is a Professor in three departments at the University of Illinois at Urbana-Champaign. His research interests focus on conservation genetics and behavioral ecology with a focus on centrarchid fishes. His findings have helped to elucidate the consequences of outbreeding depression, hybridization, and fisheries exploitation on centrarchid populations. In his role at the INHS, Dr. D. P. Philipp conducts research in support of the Illinois Department of Natural Resources. He is the director of the state creel survey and responsible for assessing recreational fishery dynamics throughout Illinois. Dr. D. P. Philipp has served on a number of committees including the Independent Scientific Advisory Board of the Northwest Power and Conservation Council. He is one of the initial founders of the Fisheries Conservation Foundation (an education and outreach partner with the American Fisheries Society) and currently serves on the Foundation’s Board of Directors. He has edited several prominent books including “Black Bass Ecology and Conservation” in 2002 and has over 100 papers in peer reviewed outlets. D. P. Philipp was selected as the first touring lecturer for the Zoological Education Trust of the Canadian Society of Zoologists. He and his family reside in Champaign, Illinois, but spend the spring in Canada studying centrarchid reproduction at the Queen’s University Biology Station.
Chapter 1
Species diversity, phylogeny and phylogeography of Centrarchidae

T. J. Near and J. B. Koppelman

1.1 Introduction

Centrarchidae is a clade of freshwater fishes endemic to North America, a part of the world that harbors more species of freshwater fishes than any other nontropical region on Earth (Briggs 1986; Lundberg et al. 2000). Centrarchid fishes have been of interest to biologists for a long period of time because they are commonly the dominant top-level predators in the diverse communities of freshwater fishes in eastern North America, and as such, they are among the world’s most popular freshwater sport fishes (Henshall 1881; Etnier and Starnes 1993; Philipp and Ridgway 2002). Interestingly, it is only in the last 10 years or so that comparative morphological and molecular data have been used in conjunction with objective character-based methods to investigate the phylogenetic relationships of Centrarchidae.

The goal of this chapter is to review and assess previous ideas regarding the diversity and relationships of centrarchid species. We hope to provide biologists from all disciplines with a clear picture of the current and best-supported hypotheses of centrarchid phylogeny, and we intend to illustrate how many recent, cutting-edge efforts have agreed remarkably with studies published as far back as the nineteenth century. Although we realize our esoteric interests in centrarchid diversity and phylogeny, as well as our desire to understand the results of modern phylogenetic analyses in the context of the rich past of centrarchid taxonomy and systematics may be confusing to the average fish biologist or ichthyologist, we will attempt to clarify what seems like a morass of trees and classifications for biologists in need of phylogenetic hypotheses. It is our desire that both comparative biologists and conservation agencies exploit the current state of knowledge regarding centrarchid diversity and phylogenetic relationships.

In this chapter we provide a discussion of the currently recognized diversity of both extant and fossil species in Centrarchidae, and we attempt to illuminate some unresolved issues in this area that need attention in future research efforts. We present an overview of previous investigations and hypotheses concerning the evolutionary relationships of Centrarchidae, including a discussion of recent efforts using morphological and molecular data in addition to those that pre-date the development of phylogenetic systematics, or cladistics (Hennig 1966). Many of the pre-cladistic ideas of centrarchid relationships discussed in this review were presented as purely taxonomic hypotheses, where the hypothesized relationships were implied from the composition and ranking of taxa.

Evolutionary biologists often investigate genetic variation within a geographic context, as intraspecific gene trees often show a strong geographic pattern. Such is the science of phylogeography (Avise 2000). We provide a review and discussion of phylogeography in centrarchids, highlighting some of the problems that have made such analyses in Centrarchidae less straightforward than in species from other groups of North American freshwater fishes.

1.2 Species diversity

1.2.1 Extant species and the status of subspecies

Currently, 34 extant species are recognized in Centrarchidae (Table 1.1), with the most recently described species being Ambloplites constellatus and Micropterus cataractae (Cashner and Suttkus 1977; Williams and Burgess 1999). As in
Table 1.1 Currently recognized centrarchid species and proposed classification. Fossil genera and species are indicated with a dagger.

<table>
<thead>
<tr>
<th>Centrarchidae (44 species: 33 extant, 11 extinct)</th>
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<td><strong>Centrarchinæ</strong></td>
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<tr>
<td><em>Acantharchus pomotis</em> (Baird 1855) Mud sunfish</td>
</tr>
<tr>
<td><em>Ambloplites ariommus</em> (Viosca 1936) Shadow bass</td>
</tr>
<tr>
<td><em>Ambloplites cavifrons</em> (Cope 1868) Roanoke bass</td>
</tr>
<tr>
<td><em>Ambloplites constellatus</em> (Cashner and Suttkus 1977) Ozark bass</td>
</tr>
<tr>
<td><em>Ambloplites ruprestris</em> (Rafinesque 1817) Rockbass</td>
</tr>
<tr>
<td><em>Archoplites †clarki</em> (Smith and Miller 1985) Clarkia perch</td>
</tr>
<tr>
<td><em>Archoplites interruptus</em> (Girard 1854) Sacramento perch</td>
</tr>
<tr>
<td><em>Archoplites †molarus</em> (Smith et al. 2000) Ringold sunfish</td>
</tr>
<tr>
<td><em>Archoplites †haylori</em> (Miller and Smith 1967) Lake Idaho sunfish</td>
</tr>
<tr>
<td>†<em>Boreocentrarchus smithi</em> (Schlaikjer 1937) Healy Creek sunfish</td>
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<tr>
<td><em>Centrarchus macropterus</em> (Lacepède 1801) Flier</td>
</tr>
<tr>
<td><em>Enneacanthus chaetodon</em> (Baird 1855) Blackbanded sunfish</td>
</tr>
<tr>
<td><em>Enneacanthus gloriosus</em> (Holbrook 1855) Bluespotted sunfish</td>
</tr>
<tr>
<td><em>Enneacanthus obesus</em> (Girard 1854) Banded sunfish</td>
</tr>
<tr>
<td>†<em>Plioplarchus septemspinosus</em> (Cope 1889) John Day sunfish</td>
</tr>
<tr>
<td>†<em>Plioplarchus sexspinosus</em> (Cope 1883) Sentinel Butte sunfish</td>
</tr>
<tr>
<td>†<em>Plioplarchus whitei</em> (Cope 1883) Laramie sunfish</td>
</tr>
<tr>
<td><em>Pomoxis annularis</em> (Rafinesque 1818) White crappie</td>
</tr>
<tr>
<td><em>Pomoxis †lanei</em> (Hibbard 1936) Ogallala crappie</td>
</tr>
<tr>
<td><em>Pomoxis †lanei</em> (Hibbard 1936) Ogallala crappie</td>
</tr>
<tr>
<td><em>Pomoxis nigromaculatus</em> (Lesueur 1829) Black crappie</td>
</tr>
<tr>
<td><strong>Lepominae</strong></td>
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<tr>
<td><em>Lepomis auritus</em> (L 1758) Redbreast sunfish</td>
</tr>
<tr>
<td><em>Lepomis cyanellus</em> (Rafinesque 1819) Green sunfish</td>
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<tr>
<td><em>Lepomis gibbosus</em> (L 1758) Pumpkinseed</td>
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<tr>
<td><em>Lepomis gulosus</em> (Cuvier 1829) Warmouth</td>
</tr>
<tr>
<td><em>Lepomis humilis</em> (Girard 1858) Orangespotted sunfish</td>
</tr>
<tr>
<td>†<em>Lepomis †kansasensis</em> (Hibbard 1936) Rhino Hill sunfish</td>
</tr>
<tr>
<td><em>Lepomis macrochirus</em> (Rafinesque 1819) Bluegill</td>
</tr>
<tr>
<td><em>Lepomis marginatus</em> (Holbrook 1855) Dollar sunfish</td>
</tr>
<tr>
<td><em>Lepomis megalotis</em> (Rafinesque 1820) Longear sunfish</td>
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<tr>
<td><em>Lepomis microlophus</em> (Günther 1859) Redear sunfish</td>
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<tr>
<td><em>Lepomis miniatus</em> (Jordan 1877) Redspotted sunfish</td>
</tr>
<tr>
<td><em>Lepomis peltastes</em> (Cope 1870) Northern longear sunfish</td>
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<tr>
<td><em>Lepomis punctatus</em> (Valenciennes 1831) Spotted sunfish</td>
</tr>
<tr>
<td><em>Lepomis †serratus</em> (Smith and Lundberg 1972) Keigh sunfish</td>
</tr>
<tr>
<td><em>Lepomis symmetricus</em> (Forbes 1883) Bantam sunfish</td>
</tr>
</tbody>
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(continued)
Species diversity, phylogeny and phylogeography of Centrarchidae

<table>
<thead>
<tr>
<th>Centrarchidae (44 species: 33 extant, 11 extinct)</th>
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</thead>
<tbody>
<tr>
<td>Micropterinae</td>
</tr>
<tr>
<td>Micropterus cataractae (Williams and Burgess 1999) shoal bass</td>
</tr>
<tr>
<td>Micropterus coosae (Hubbs and Bailey 1940) Redeye bass</td>
</tr>
<tr>
<td>Micropterus dolomieu (Lacepède 1802) smallmouth bass</td>
</tr>
<tr>
<td>Micropterus floridanus (LeSueur 1822) Florida bass</td>
</tr>
<tr>
<td>Micropterus henshali (Hubbs and Bailey 1940)</td>
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<tr>
<td>Micropterus notius (Bailey and Hubbs 1949), Suwannee bass</td>
</tr>
<tr>
<td>Micropterus punctulatus (Rafinesque 1819) spotted bass</td>
</tr>
<tr>
<td>Micropterus †relictus (Cavender and Smith 1975) Chapala bass</td>
</tr>
<tr>
<td>Micropterus salmoides (Lacepède 1802) largemouth bass</td>
</tr>
<tr>
<td>Micropterus treculi (Vaillant and Bocourt 1874) Guadalupe bass</td>
</tr>
</tbody>
</table>

many groups of animals, there are many more scientific names available than there are recognized species. Not including the names of valid extant species (Table 1.1), there are 118 nominal names that are considered synonyms for species in Centrarchidae. Of these, 11 were either new names for subspecies or were introduced as species names and have been used at some point to designate subspecies (Gilbert 1998). Of the 118 nominal names, 9 are based on hybrid centrarchids; all but 1 of these are the hybrid combinations of *Lepomis cyanellus* * L. macrochirus* and *L. cyanellus* * L. gibbosus* (Hubbs 1920; Hubbs and Hubbs 1932; Gilbert 1998).

The contemporary view of species diversity in Centrarchidae was fairly well settled by the turn of the nineteenth and twentieth centuries, as the vast majority of valid centrarchid species were described between 1800 and 1883 (Table 1.1; Figure 1.1). This period was also when most of the synonymous names were introduced (Bailey 1938; Gilbert 1998). Through both the nineteenth and twentieth centuries centrarchid species have been described using very similar types of data from external morphology, including meristics (scale row and fin element counts), morphometrics (body proportions), pigmentation patterns, and coloration (Cope 1868, 1870; Hubbs and Bailey 1940; Cashner and Suttkus 1977; Williams and Burgess 1999). To date, comparative phylogenetic methods, using either morphological or molecular data, have not been used in describing new centrarchid species.

![Figure 1.1](image_url) Plot illustrating the growth of valid extant centrarchid species descriptions from the nineteenth through twentieth centuries. *Ambloplites rupestris* redrawn from Forbes and Richardson (1920).
The status of subspecies in Centrarchidae is much less resolved when compared to the 33 recognized valid extant species (Table 1.1). The use of subspecies in North American fish taxonomy has a relatively inconsistent history, and since the initial critique of subspecies, most modern workers in systematics have been moving away from using this rank (Wilson and Brown 1953; Burbrink et al. 2000). However, there remain 11 names that have been historically designated as centrarchid subspecies. We are able to categorize each of these names into three classes: (i) subspecies that do not exhibit significant variation from the nominal subspecies, (ii) subspecies that are based on hybrid specimens, and (iii) subspecies that merit elevation to species.

Three centrarchid subspecies have been invalidated as it was demonstrated that they did not differ appreciably from other populations of the nominal species. *Acantharchus pomotis mizelli* Fowler and *Enneacanthus chaetodon elizabethae* were both described as subspecies in the 1940s based on six or seven specimens (Bailey 1941; Fowler 1945). In both cases, subsequent analyses that included many more specimens failed to reveal geographic variation consistent with the recognition of the subspecies proposed for each of these species (Sweeney 1972; Cashner et al. 1989). A similar situation exists for the Neosho Smallmouth Bass, *Micropterus dolomieu velox* Hubbs and Bailey. This subspecies was described based primarily on slight differences in counts of the second dorsal fin rays, pigmentation patterns, and dentition on the tongue (Hubbs and Bailey 1940). The validity of *M. d. velox* was subsequently dismissed on the basis of slight morphological differences and clinal gradation into the nominal *M. dolomieu* (Hubbs 1956; Gilbert 1998), a conclusion supported by more recent analyses of nuclear gene encoded allozymes and mitochondrial DNA (mtDNA) sequence data (Stark and Echelle 1998; Kassler et al. 2002).

At least one centrarchid subspecies has turned out to be based on hybrid specimens. *Micropterus punctulatus wichitae* Hubbs and Bailey was described as a subspecies from the Wichita Mountains of southwestern Oklahoma based on differences in scale row counts (Hubbs and Bailey 1940). However, this population was initially described as hybrids of *M. punctulatus* and *M. dolomieu* (Hubbs and Ortenburger 1929). Morphological data from *M. p. punctulatus*, *M. p. wichitae*, and *M. dolomieu* and historical records of nommative *M. dolomieu* introductions near the type locality of *M. p. wichitae* support the hypothesis that this subspecies is based on hybrid *M. punctulatus* *M. dolomieu* specimens (Cofer 1995). Genetic analysis of both nuclear and mtDNA in *M. punctulatus* populations from the Red and Arkansas River Basins did not reveal genetic divergence of the Wichita Mountain populations of *M. punctulatus* (Coughlin et al. 2003).

*Lepomis megalotis* and *L. macrochirus* are two centrarchid species that are thought to be polytypic and contain described subspecies (Mayden et al. 1992; Gilbert 1998). Future research documenting morphological and genetic variation in these two complexes has the strong possibility to result in the recognition of additional valid centrarchid species. *L. megalotis* has four, and possibly seven, valid subspecies, *L. m. megalotis* (Rafinesque), *L. m. aquilensis* (Baird and Girard), *L. m. breviceps* (Baird and Girard), and *L. m. occidentalis* Meek (Bailey 1938). In addition, *L. m. convexifrons* (Baird and Girard), *L. m. fallax* (Baird and Girard), and *L. m. popeii* (Girard) are three additional forms from Texas that may represent other unrecognized species related to *L. megalotis* (Gilbert 1998). Unfortunately, there is no published analysis of morphological variation among these subspecies, but a Ph.D. dissertation had detected substantial morphometric variation among four of the described subspecies (Barlow 1980). An analysis of allozyme variation detected appreciable genetic divergence of *L. m. breviceps* and *L. m. aquilensis* relative to the other subspecies (Jennings and Philipp 1992). Based on morphometric and body size differences, *L. pelustes* Cope was elevated as a species from a subspecies of *L. megalotis* (Bailey et al. 2004). We suspect that several additional centrarchid species will be recognized as a result of analyses of geographic variation and phylogeny of the *L. megalotis* complex using comparative morphological and molecular data.

There is a degree of uncertainty as to how many subspecies of *Lepomis macrochirus* are recognized. The problem centers on *Pomotis speciosus* described from Brownsville, Texas by Baird and Girard (1854). This species was subsequently synonymized with *L. macrochirus* by Hubbs (1935). At a later date, Hubbs and Lagler (1958) treated *P. speciosus* as a subspecies of *L. macrochirus*, concluding that the geographic range is throughout Texas and northeastern Mexico. Allozyme analyses did not detect genetic differentiation between *L. m. macrochirus* and *L. m. speciosus* (Kulzer and Greenbaum 1986), and subsequent treatments of centrarchid species diversity have not recognized *L. m. speciosus* (Gilbert 1998).

The two valid subspecies of *L. macrochirus* present an interesting problem of nomenclature confusion, morphological and genetic divergence, an area of presumed secondary contact and introgression, and a biogeographic pattern and a timing of divergence seen in another centrarchid sister species pair. The nominal subspecies *L. m. macrochirus* Rafinesque is distributed across eastern North America except for the northern Atlantic Coast (Lee et al. 1980), while the other subspecies is endemic to the Florida Peninsula (Fellley 1980). Initially, the subspecies found in Florida was designated as *Lepomis*
Macrodipterus purpurescens Cope under the premise that this subspecies extended from the Atlantic Coast of the Carolinas to the Florida Peninsula (Hubbs and Allen 1943; Hubbs and Lagler 1958). The type locality for Lepomis purpurescens is in the Yadkin River Drainage in North Carolina (Cope 1870). Subsequent morphological and molecular analyses demonstrate that this is far north of the range of the Florida subspecies (Avise and Smith 1974a; Felley 1980; Avise et al. 1984), and as Gilbert (1998) has pointed out, Cope described a Bluegill from Florida, Lepomis mystacalis (Cope 1877). Therefore, the appropriate name for the Florida Bluegill is L. macrochirus mystacalis.

Lepomis m. macrochirus and L. m. mystacalis are morphologically and genetically distinct, but there is a presumed area of introgression through secondary contact along most of southern Georgia and South Carolina (Felley 1980; Avise et al. 1984). Another sister species pair in Centrarchidae, Micropterus salmoides and Micropterus floridanus, exhibit a very similar distribution and area of secondary contact and introgression (Bailey and Hubbs 1949; Philipp et al. 1983). Based on a fossil calibrated molecular phylogeny of Centrarchidae, the divergence time between M. salmoides and M. floridanus is approximately 2.8 million years ago (mya) (Near et al. 2003, 2005b). Lepomis m. macrochirus and L. m. mystacalis exhibit a very similar divergence time. We found mtDNA cytochrome b gene sequences in Genbank for five individuals of L. m. macrochirus and a single L. m. mystacalis (accession numbers: AY115975, AY115976, AY225667, AY828966, AY828967, and AY828968). The average genetic distance between these two subspecies was 4.5%, which translates to a divergence time of roughly 2.3 mya (Near et al. 2003). Future work should aim toward gathering sufficient morphological and molecular data to more precisely determine the geographic distribution of these two forms and assess if L. mystacalis is a valid species.

Recently Micropterus henshalli (Hubbs and Bailey) was elevated as a valid species (Baker et al. 2008), but was long recognized as a subspecies of M. punctulatus (Hubbs and Bailey 1940). Micropterus henshalli is endemic to the Mobile Basin and there are slight morphological differences between populations above and below the Fall Line (Gilbert 1973; Baker et al. 2008). However, there are substantial differences in several meristic characters between M. henshalli and M. punctulatus (Gilbert 1973), and there are marked differences in body proportions and surprising life history and dietary differences between these two species (Gilbert 1973). Perhaps the most compelling evidence for the recognition of M. henshalli includes measures of genetic divergence and the results of phylogenetic analyses. Among 19 polymorphic allozyme loci surveyed for all Micropterus species, not a single allele was shared exclusively between M. henshalli and M. punctulatus, and a fixed unique allele was found in M. p. henshalli (Kassler et al. 2002). In a phylogenetic analysis of Micropterus species using gap coded continuous morphological characters M. henshalli and M. punctulatus did not form a clade (Harbaugh 1994), and these two species were sister lineages in frequency parsimony of allozyme alleles (Kassler et al. 2002). In addition, molecular phylogenetic analyses of mtDNA sequences from cytb and ND2 resulted in tree topologies where M. henshalli was nested within M. coosae and distantly related to M. punctulatus (Kassler et al. 2002). Given the evidence presented above, the classification of M. henshalli as a subspecies of M. punctulatus was not compelling and the recognition of this species is supported by the substantial comparative data.

1.3 Centrarchid fossils

The fossil record of Centrarchidae is fairly rich and extends in geologic time from the Late Eocene to Early Oligocene of approximately 35 mya to the very early Holocene of approximately 10 years ago. Both extant centrarchid species and centrarchid fossils are found only in North America, indicating that origin and diversification of this clade did not involve other continental regions. There are 11 valid and extinct centrarchid species known only from fossil material (Table 1.1; Figures 1.2–1.17), and there are fossils of seven extant species.

Despite an excitingly abundant centrarchid fossil record, at least four of the oldest fossil centrarchid species are generally unknown to science. These fossil species are undescribed and have been under study for at least three decades. Unfortunately, they have not been made available to other researchers for study, which has significantly hindered progress in understanding the evolutionary origin of Centrarchidae and its patterns of diversification. The meager information available for these four undescribed fossil species that we present here is from general synopses of the fossil record of North American freshwater fishes (Cavender 1986, 1998). The first of these four we call the High Plains Sunfish, from the northwestern part of Montana near the foothills of the Rocky Mountains. Cavender (1986, 1998) indicates that they are found in Late Eocene to Early Oligocene deposits, but more precise age estimates are unavailable. The High Plains Sunfish has three anal spines and an emarginate caudal fin. The second of these undescribed fossils is the Chadron Sunfish
†Plioplarchus sexspinosus

Figure 1.2 Photos and drawings of fossil Centrarchidae species: †Plioplarchus sexspinosus Sentinel Butte Sunfish, photo redrawn from Eastman (1917).

†Plioplarchus whitei

Figure 1.3 Photos and drawings of fossil Centrarchidae species: †Plioplarchus whitei Laramie Sunfish, redrawn from Cope (1884).

†Plioplarchus septemspinosus

Figure 1.4 Photos and drawings of fossil Centrarchidae species: †Plioplarchus septemspinosus John Day Sunfish, photo redrawn from Eastman (1917).

†Boreocentrarchus smithi

Figure 1.5 Photos and drawings of fossil Centrarchidae species: †Boreocentrarchus smithi Healy Creek Sunfish, redrawn from Schlaiikjer (1937).
Species diversity, phylogeny and phylogeography of Centrarchidae

Figure 1.6  Photos and drawings of fossil Centrarchidae species: *Pomoxis †lanei* Ogallala Crappie, photo redrawn from Hibbard (1936).

Figure 1.7  Photos and drawings of fossil Centrarchidae species: *Pomoxis †sp.* Wakeeney Crappie, redrawn from Wilson (1968).

Figure 1.8  Photos and drawings of fossil Centrarchidae species: *Archoplites †clarkii* Clarkia Perch, photo provided by Smith (1963).

Figure 1.9  Photos and drawings of fossil Centrarchidae species: *Archoplites †taylori* Lake Idaho Sunfish, redrawn from Miller and Smith (1967).
Figure 1.10  Photos and drawings of fossil Centrarchidae species: *Archoplites †molarus* Ringold Sunfish, redrawn from Smith *et al.* (2000).

Figure 1.11  Photos and drawings of fossil Centrarchidae species: *Lepomis †kansasensis* Rhino Hill Sunfish, photo redrawn from Hibbard (1936).

Figure 1.12  Photos and drawings of fossil Centrarchidae species: *Lepomis †serratus* Keigh Sunfish, redrawn from Smith and Lundberg (1972).
**Figure 1.13** Photos and drawings of fossil Centrarchidae species: *Lepomis †sp.* A Valentine Sunfish, redrawn from Smith (1962).

**Figure 1.14** Photos and drawings of fossil Centrarchidae species: *Lepomis †sp.* B Wakeeney Sunfish, redrawn from Wilson (1968).

**Figure 1.15** Photos and drawings of fossil Centrarchidae species: *Micropterus †relictus* 1975 Chapala Bass, redrawn from Smith *et al.* (1975).

**Figure 1.16** Photos and drawings of fossil Centrarchidae species: *Micropterus †sp.* B Wakeeney Bass, redrawn from Wilson (1968).

**Figure 1.17** Photos and drawings of fossil Centrarchidae species: *Micropterus †sp.* C Laverne Bass, redrawn from Smith (1962).
from Lower Oligocene limestone deposits in the South Dakota Badlands, dating this fossil to the White River group of approximately 28 to 35 mya (Tedford et al. 1987). The Chadron Sunfish has three anal spines and 27 to 28 vertebrae (Cavender 1986). The third fossil sunfish in this group of undescribed forms is from Lower Miocene deposits in South Dakota, and Cavender (1986) provides an age of approximately 25 mya. These are very similar in morphology to the Chadron Sunfish, but have 29 vertebrae (Cavender 1986). The last of the four undescribed fossils in Cavender (1986) is from Middle Miocene deposits, but no location is given. This fossil species has six or seven anal fin spines and is similar to fossils that were assigned to †Plioplarchus (Cope 1884).

There are two extinct genera of Centrarchidae known from the fossil record, †Plioplarchus and †Boreocentrarchus. †Plioplarchus contains three species (Table 1.1), and is the oldest of the described centrarchid fossils (Figures 1.2–1.4). †Plioplarchus sexspinosus and †P. whitei were described from Oligocene age freshwater limestone deposits from the Sentinel Butte of North Dakota (Cope 1883) that date to approximately 30 mya (Feldman 1962) (Figures 1.2 and 1.3). †Plioplarchus sexspinosus and †P. whitei are also found in the Badlands of South Dakota in the White River Group. Specimens that are either †P. sexspinosus or †P. whitei are found at the contact between the Chadron and Brule Formations (Welzenbach 1992), and this is dated to approximately 31 mya (Tedford et al. 1987). †Plioplarchus septemspinosus was described from the John Day River in Oregon (Cope 1889) in the geological deposits that make up the John Day Fauna (Figure 1.4), and is dated between 18 and 31 mya (Tedford et al. 2004). Fossils currently assigned to †P. septemspinosus are also found in the Trout Creek Flora in Oregon and this is dated at 13 mya (Graham 1999). Morphological analyses indicate that †P. septemspinosus from the John Day and Trout Creek locations in Oregon are different from each other and both of these are quite divergent from †P. sexspinosus and †P. whitei (Schlaikjer 1937; Bailey 1938; Smith and Miller 1985). These differences were substantial enough for Bailey (1938) in his unpublished Ph.D. dissertation to describe a new genus for †P. septemspinosus.

†Boreocentrarchus smithi was described from Healy Creek, Alaska in deposits that were thought to age from the Oligocene to the Early Miocene (Figure 1.5) (Schlaikjer 1937; Uyeno and Miller 1963), and a more precise estimate of this formation at 24 to 18 mya agrees with these earlier estimates (Merritt 1987). Schlaikjer (1937) argues that †B. smithi is closely related to †P. septemspinosus, but others have questioned whether †B. smithi is a centrarchid (Uyeno and Miller 1963). Both †Plioplarchus and †Boreocentrarchus are classified in the Centrarchinae (Table 1.1), because these species possess more than three anal fin spines. Undescribed fossil species in this clade include one from the Horse Creek Fish Quarry in Laramie Co., Wyoming, that dates to approximately 19 mya (Cassiliano 1980), another from the Bear Valley, California (Smith and Miller 1985), and a third from the Humboldt Formation, Nevada, that dates to 9 mya (Smith and Miller 1985; Smith et al. 2002).

The remaining centrarchid fossil species are classified in genera that also contain extant species (Table 1.1). Pomoxis is known from the fossil record with one described species, P. †lanei, and one undescribed fossil species. Pomoxis †lanei was found in the Rhino Hill Quarry in Logan Co., Kansas (Hibbard 1936), and age of this fossil formation is correlated with Coffee Ranch mammals that date to 6.6 mya (Wallace 1997; Passey et al. 2002). The holotype of P. †lanei is a complete and crushed skeleton (Figure 1.6). The specimen is a remarkable impression and many morphological features can be scored, counted, or measured (Hibbard 1936). The phylogenetic position of P. †lanei in Pomoxis is unresolved due to conflicting characters. The presence of seven dorsal fin spines and a long dorsal fin base supports the hypothesis that P. †lanei and P. nigromaculatus are sister species (Smith 1962). However, the hypothesis that P. nigromaculatus and P. annularis are sister species is supported by the presence of 17 to 20 anal fin rays in these species versus 12 anal fin rays in P. †lanei (Uyeno and Miller 1963). There is a second fossil species of Pomoxis that is undescribed. These fossils were found in the Wakeeney local fauna that is a part of the Ogallala Formation in Kansas (Wilson 1968). The age of this formation was placed in the lower portion of the Ash Hollow or upper Valentine Formation (Wilson 1968), and this dates to approximately 12 mya (Tedford et al. 2004). These are the oldest Pomoxis fossils and they are fragmentary, consisting of a dentary and premaxillary fragments (Figure 1.7).

Archoplites contains three fossil species and only one extant species (Table 1.1). The oldest of the Archoplites fossil species is A. †clarki from the Clarkia Lake Beds in Idaho (Figure 1.8) (Smith and Miller 1985). This fossil formation has been dated at 15.5 mya (Golenberg et al. 1990; Wing 1998). Archoplites †taylori is found in seven different fossil locations in southwestern Idaho and these sites are characterized as lacustrine deposits (Figure 1.9). The oldest of the fossil sites containing A. †taylori is the Poison Creek formation and is dated at 9 mya (Smith and Cossel 2001). The youngest formation containing A. †taylori fossils is Jackass Butte, a part of the Grandview local fauna dated at 2.2 mya (Smith 1975; Lundelius et al. 1987). Archoplites †molarus was recently described from the Ringold Formation.