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THE WILDERNESS OF PANBIOGEOGRAPHY:  
A SYNTHESIS OF SPACE, TIME, AND FORM?

**Panbiogeography Special Issue.**—1990. New Zealand Journal of Zoology 16(4):iii + 471-815. DSIR Publishing, P.O. Box 368, Lawrence, Kansas 66044, and P.O. Box 9741, Wellington, New Zealand. \$45.00 (US), \$45.00 (NZ).

Biogeography is a diverse field of study; its objectives are the elucidation of distributions and the determination of the factors structuring these patterns, both past and present. Implicit in this characterization is that to understand the distribution of any organism one should be cognizant of both recent and historical factors operating at both the microevolutionary and macroevolutionary scales. Biogeography is unlike most areas of biology in that most investigators are not trained as biogeographers but are either systematists or ecologists. This dichotomy in profession has resulted in a fundamental dichotomy of theories invoked to explain the evolution of organisms and the acquisition of their distributions using either historical or ecological scenarios. Minimal attention has been given to a synthesis of both fields wherein microevolutionary processes (e.g., dispersal, extinction) are considered on the historical scale and macroevolutionary processes (e.g., patterns of speciation, phylogenetic constraints) are considered on the ecolog-

ical scale. To accomplish the primary objective of biogeography, a more holistic evolutionary approach to the science is needed. Undoubtedly, both ecological and historical factors are influential in determining the distributions of organisms. However, frequently investigators confuse these explanations in attempts to explain the varied scale of naturally occurring patterns, invoking either set of processes inappropriately. Ecological principles are posited to account for species distributions, replicated biogeographic patterns, and community structure. Likewise, historical explanations have traditionally lacked the latitude to incorporate ecological/dispersal explanations. Panbiogeography (Greek *pan*—meaning *all* and *every*, used to denote the entirety of a diversified group) is a school of thought in biogeography founded by Leon Croizat that advocates a holistic approach to this science through the incorporation of ecological, geological, and systematic information in the study of organisms in space, time, and form.

*Panbiogeography Special Issue* represents a collection of papers on the New Zealand biota, assembled to advance the panbiogeographic method and communicate perceived problems in other contemporary approaches in biogeography. This special issue of the *New Zealand Journal of Zoology* is the culmination of a special symposium held in Wellington, New Zealand, in May 1988. The anticipated objective of the volume was, as stated in the foreword by Craw, to demonstrate the relevance of panbiogeography to New Zealand natural history. After reading the volume, I would recognize other objectives, including (1) to present a general review of the biogeography and the unique nature of the New Zealand biota, (2) to present a historical review and evaluations of biogeographic interpretations and classifications for the evolution of the biota, (3) to communicate inadequacies of most historical and contemporary biogeographic methods and interpretations, both empirical and philosophical, and (4) to reevaluate and revitalize panbiogeography of Croizat as a complete approach to understanding the evolution of the earth and its biodiversity.

Even a cursory reading of this volume indicates that New Zealand is a complex and apparently composite series of land masses containing a complex flora and fauna with "affinities" to many different mainlands and islands. Although this "biota problem" is in no way unique relative to other continental and island faunas, resolving the historical development of a biota of this nature is complicated. Using contemporary taxonomies of species or supraspecific taxa, affinities are identified with Holarctic regions, Malayo-Pacific, Australian, South American, African, antitropical Pacific, and others. Another subset of the biota includes taxa that are either endemic to New Zealand (with or without known closest relatives) or are cosmopolitan in distribution and about which there is limited biogeographic information. Nearly every author in the volume discusses the complexities of this biogeography, how the complexities have been viewed historically by different scientists, and how the origin of this complex biota is best understood within the panbiogeographic research paradigm.

The symposium volume is introduced with a fore-

word by R. Craw. In addition to providing a general review of the coming contributions, the general philosophy of panbiogeography is briefly described, and the significance of the method/theory and the New Zealand "school" of biogeographers to modern biology is emphasized. Craw summarizes the panbiogeography doctrine as

an approach to biology that focuses on the role of place/locality in the *evolutionary process*. It stresses that an understanding of place/locality is a fundamental precondition for any adequate analysis of *processes* involved in *evolutionary change*. Central to the panbiogeographic project is an acknowledgment of the *uniqueness* and *singularity* of different places/localities/organisms, without denying the view that their *evolutionary history* also reflects the *interaction of general processes*. Panbiogeography emphasises the role of place in the *processes of the past* as understood from the perspective of the present.

In this quote, the emphasis is mine. The italicized key words/phrases emphasize the number of times that the use of historical processes, phylogenetic history, and/or phylogenetic constraint is acknowledged for a complete understanding of the geography of biotas. This preamble to the panbiogeographic project is significant because given this characterization one would expect to find, in addition to distributional information, a necessary dependence upon or interest in genealogical relationships of organisms in the panbiogeographic research program. Apparently, most contributors (including Craw) do not agree with this characterization of the traditional or modern panbiogeographic philosophy. The perceived significance and actual use of any genealogical inference in biogeography is largely neglected in the following contributions. Instead, there is a reliance upon existing taxonomic classifications, geographic proximity, and phenetic similarities in geography as measures of evolutionary history.

The opening contribution by R. D. M. Page offers a brief review of the intriguing and complex nature of the New Zealand biota, an evaluation as to why this flora and fauna has stimulated so much controversy in the past, and an acknowledgment that the biogeographers of this region have been responsible for "some exciting, if somewhat unorthodox ideas on biogeography." Explanations for the composite history of the biota have been plagued by many different concepts before and after the discovery of plate tectonics involving land bridges, dispersal, vicariance, and biotic amalgamation. Page briefly reviews the systematic and biogeographic significance of the ideas developed by Hennig, Croizat's restructuring of biogeography to include "ecology, geology, and systematics" in a regional classification of biotas involving ocean basins, and the synthesis of these ideas in the formation of vicariance biogeography by "The New York School." Additional discussion focuses on some criticisms of the vicariance/dispersal controversies, the notion that taxonomic and geographic congruence are different concepts, analytical methods developed by the New Zealand project, and the need for future studies to stress geology and geomorphology.



## Systematics and Biogeography of Snubnose Darters, Genus *Etheostoma* (Teleostei: Percidae) from the Black Warrior River System, Alabama

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**Key Word Index**—Percidae; *Etheostoma*; snubnose darters; allozyme variation; speciation; systematics; biogeography.

**Abstract**—Members of the *Etheostoma chermocki* species group, formerly known only as the Warrior snubnose darter, were examined from throughout their ranges for products of 44 presumptive gene loci. Polyallelic loci support the specific recognition of *E. chermocki* and indicate that *E. bellator* is actually a composite of three distinct evolutionary species diagnosable on the basis of both fixed allelic products and significant allele frequency differences. Based on other studies, these species are also diagnosable using traditional morphological characteristics. *Etheostoma bellator* is the most widely distributed species, while the two new species are endemic to the upper Sipsey and Locust forks of the Black Warrior River system. Phylogenetic evaluation of 30 variable loci and all possible bifurcating trees indicate that the *E. chermocki* species group is not a monophyletic assemblage. Rather, some species of the group are more closely related to *E. simoterum* and *E. ramseyi* in the Tennessee and Alabama river drainages, respectively. Diversification within the *Etheostoma chermocki* species group was probably associated with the complex break-up of the Appalachian River System, once connecting the upper Tennessee River and rivers of the current Mobile Basin, and drainage exchanges between the Locust Fork of the Black Warrior River and the adjacent Cahaba or Coosa rivers. Copyright © 1996 Elsevier Science Ltd

### Introduction

The *Etheostoma chermocki* species group is endemic to the Black Warrior River System in Alabama (Fig. 1) and includes *E. chermocki* Boschung, Mayden, and Tomelleri and *E. bellator* Suttkus and Bailey. For over 30 years this group has been referred to as a single undescribed species, the Warrior snubnose darter. Only recently has the natural diversity within this group received taxonomic attention through morphological studies by Boschung *et al.* (1992) and Suttkus and Bailey (1993). Neither study examined the complex for phylogenetic relationships or for divergence at the molecular level.

The description of *E. bellator* by Suttkus and Bailey (1993) did not include, for some characters, an evaluation of all known groups of disjunct subpopulations within the species. The description was based primarily upon materials from Murphy Creek in Mulberry Fork and Valley Creek in the lower Black Warrior River, but excluded populations from both the Sipsey and Locust forks of the Black Warrior River (Fig. 1). Recent comparisons within the *E. chermocki* group (Mayden and Kuhajda, unpubl. data) have revealed significant morphological and coloration character divergence

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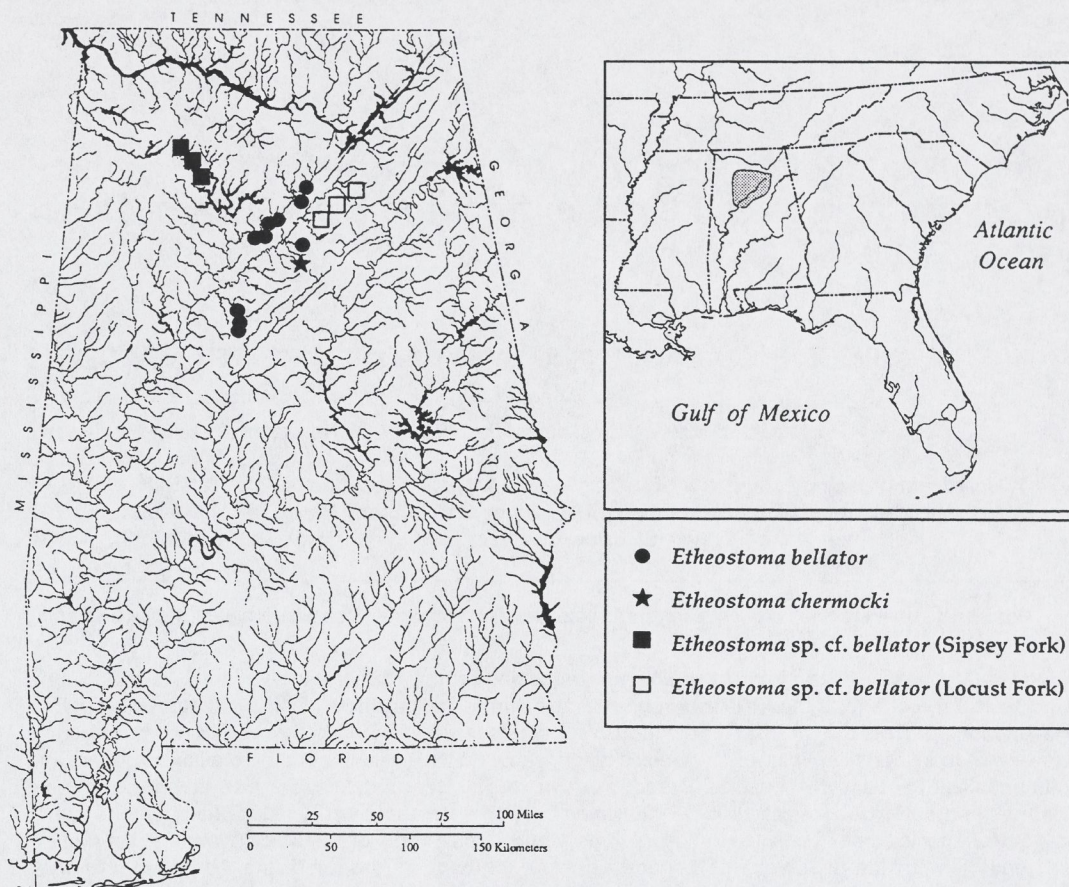


FIG. 1. DISTRIBUTION OF MEMBERS OF THE *ETHEOSTOMA CHERMOCKI* SPECIES GROUP. Shaded area of inset map (right) illustrates area of interest in the southeastern United States.

within *E. bellator* from both the Sipsey and Locust Forks of the Black Warrior River. This diversity was not revealed in any previous studies of the species, including the original description of *E. bellator* by Suttkus and Bailey (1993).

We present an analysis of genetic variation within the *E. chermocki* species group sampled from throughout the disjunct geographic ranges of its members. Our survey of allozyme variation not only supports the validity of *E. chermocki* but unambiguously supports a more restricted *E. bellator* and two new species masquerading within *E. bellator*. The geographic pattern of diversification within "*E. bellator*" at the allozyme level is concordant with diversity revealed through morphological studies (Mayden and Kuhajda, unpubl. data). The previously unrecognized species have restricted distributions in the upper Sipsey Fork and the upper Locust Fork of the Black Warrior River System, and warrant detailed biological investigations, status surveys, and protection. Complete descriptions of the two new species, *E. sp. cf. bellator* (Sipsey Fork) and *E. sp. cf. bellator* (Locust Fork) will be published elsewhere (Mayden and Kuhajda, unpubl. data).

### Materials and Methods

Methods for allozyme electrophoresis and data analysis generally followed those described by Wood and Mayden (1992) and Mayden and Matson (1992). Enzyme and buffer systems are presented in Table 1. *BIOSYS-1* (Swofford and Selander, 1981), *FREQPARS* (Swofford and Berlocher, 1987), and *PAUP* (version 3.1.1; Swofford, 1993) were employed in population genetic and phylogenetic analyses. Two types of phylogenetic analyses of species were conducted. First, phylogenetic analysis of discretely-coded allozyme characters (*sensu* Buth, 1984) employed *PAUP*; analyses involved the *EXHAUSTIVE* search