



BODY SHAPE EVOLUTION AND TROPHOTAENIAL VARIATION WITHIN THE
GOODEIDAE

By
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A Thesis
Submitted to the Faculty of
Southeastern Louisiana
University
in Partial Fulfillment of the Requirement
for the Degree of Master of Science
in Biology

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June 2016

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WITHIN THE GOODEIDAE

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The goodeids (Teleostomi: Cyprinodontiformes) are a family of freshwater fishes that have a disjunct distribution. Throughout their initial discovery many features have made them characteristic of adaptive radiation and diversification although little work has been done on the family as a whole. The subfamily Goodeinae inhabit the Mesa Central of Mexico, are viviparous, sexually dimorphic, and possess unique pre-placenta like structures called the trophotaeniae. The other subfamily, the Empetrichthyinae, are found in the Great Basin, and exhibit oviparity. The differences between the two subfamilies makes them an excellent group for evolutionary study. One focus of the thesis is to determine if the disparities between the two lineages correlate with differences in their rate of body shape evolution by utilizing geometric morphometrics. Additionally, a re-evaluation of the goodeid characters currently used as the accepted view of higher level taxonomic classification, will be facilitated using a higher resolution approach (SEM) to determine if they are in fact diagnostic of the taxa and genera within the subfamily. This

proposal aims to better our understanding of the family as a whole, applying phenotypic, ecological, and diversification data to better to conserve this unique group of fishes.

Keywords: Goodeidae, geometric morphometrics, trophotaeniae, radiation, habitat

PREVIEW

ACKNOWLEDGEMENTS

I would like to thank Dr. Kyle R. Piller for his constant advisement, guidance and wisdom throughout this whole process. Even throughout this past year which brought many hurdles to cross. I would also like to extend my gratitude to my committee members Dr. Gary Shaffer and Dr. Brian Crother for their help and encouragement. Pat Hartman, thanks to your contributions and help throughout this process, without you much of this data would be lost. I would like to dedicate this thesis to my twin brother, Charles Evans Foster II, although he may never read it.

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PREVIEW

CHAPTER I

BODY SHAPE EVOLUTION AND TRAIT MODULARITY WITHIN THE
GOODEIDAE (CYPRINODONTIFORMES)

Introduction:

Disproportionate species richness between clades is one of the most interesting patterns in evolutionary biology, with some clades being exceedingly species rich while others are relatively depauperate. The drivers of speciation and diversification have been an ongoing discussion within the literature for decades (Thorson, 1957; Hutchinson, 1959; Fischer, 1960; Foote, 1993a; Losos & Miles, 2002; Burbrink *et al.*, 2012). Although species richness is expected to vary purely by stochastic processes, many other ideas have been put forth to explain discrepancies in species richness. First, clade age is believed to be important, whereas older clades are expected to have higher species richness due to the greater length of time for diversification and speciation to occur (McPeck & Brown, 2007; Bloom *et al.*, 2014). Second, it has been shown that differential diversification rates are a common explanation for clade disparity (Cook & Lessa, 1998; Magallon & Sanderson, 2001; Ricklefs, 2007). Differential speciation and extinction rates are often correlated with phenomena such as key innovations and adaptive radiations (Erwin, 1992; Foote, 1993b; Heard & Hauser, 1995; Hunter, 1998). In fact, the majority of the most heavily studied examples of adaptive radiation are related to trophic and/or habitat specializations (Greenwood, 1973; Losos, 1990; Chakrabarty, 2005).

n extension of clade disparity is that species rich clades should harbor higher levels of phenotypic diversity in comparison to less speciose clades. Morphological disparity and speciation may be linked, and one hypothesis suggests that clades with higher rates of phenotypic evolution may be able to reach into novel ecological trait space leading to an increase in diversification (Parent & Crespi, 2009; Slater *et al.*, 2010; Martin & Wainwright, 2011). The idea that some organisms are more morphologically versatile than others leading to replacement of the later, is a key concept in the idea of ecological opportunity and adaptive zones (Simpson, 1944; Vermeiji, 1973; Schluter, 2000). Ecological opportunity may arise after extinctions, for example, whereby the remaining taxa spread into morphospace previously occupied by the extinct taxa (Foote, 1997).

The freshwater fish family Goodeidae (Jordan, 1923) (Order: Cyprinodontiformes) are an ideal group to address the process of diversification. They are found within the southwestern United States and the central Mexican highlands (Figure 1). The disjunct distribution of taxa in the Great Basin and central Mexico is unique to Goodeidae, and found in no other primarily freshwater fish groups. Increasing desiccation of the Sonoran Desert during the Tertiary is hypothesized to have split the ancestral goodeid into two disjunct subfamilies (Parenti, 1981; Webb *et al.*, 2004), the Goodeinae (Jordan, 1923) and the Empetrichthyinae (Jordan *et al.*, 1930). The subfamily Goodeinae is endemic to Mexico with approximately 18 genera and 40 species, with the highest diversity occurring in the geographic area known as Mesa Central, a relatively depauperate, isolated highland plateau (Doadrio & Domínguez-Domínguez, 2004; Miller *et al.*, 2005; Domínguez-Domínguez *et al.*, 2010). This region has been subjected to

substantial volcanic and tectonic activity since the beginning of the Miocene leading to intricate hydrological systems (Nieto-Samaniego *et al.*, 1999; Dominguez-Dominguez, *et al.*, 2006), which have likely contributed to higher speciation in this area (Domínguez-Domínguez *et al.*, 2010). All species in the subfamily are viviparous and embryos of all species possess a vascular rectal structure, known as a trophotaniae, for nutrient absorption (Hubbs & Turner, 1939; Wourms & Cohen, 1975; Cohen, 1976; Lombardi & Wourms, 1988). Across the Goodeinae, the species utilize diverse trophic ecologies ranging from strictly carnivorous (*Allophorus robustus* and *Allodontichthys tamazulae*), to herbivorous (*Goodea atripinnis*), however the majority of the species occupy the trophic spectrum between these two dietary extremes. Species of Goodeinae inhabit lakes, creeks, marshes, canals, and large rivers (Miller *et al.*, 2005), with some species being habitat specialists (i.e. springs only) and others being more generalist in terms of their habitat preferences. Sexual dimorphism is marked with males often displaying elaborate colorful dorsal, anal, and caudal fins relative to females.

The sister group to the Goodeinae, the subfamily Empetrichthyinae is much less diverse than the Goodeinae. Two genera, *Crenichthys* and *Empetrichthys*, and three species (and multiple subspecies) currently occupy the Great Basin (Figure 1). Several additional species have gone extinct within the last century (Minckley & Deacon, 1968; Grand & Riddle, 1983; Williams, 1996). All species of Empetrichthyinae lack sexual dimorphism, are oviparous instead of giving live-birth, are opportunistic omnivores (Williams & Williams, 1982; Wilde, 1989) and utilize similar niches in springs and pools of the Great Basin of the United States (Williams & Williams, 1982; Vigg, 1982).