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REVIEW OF TAXONOMY AND ZOOGEOGRAPHY OF ATHERINIFORM FISHES IN THE FLORIDA KEYS, WITH COMMENTS ON POPULATIONS IN PENINSULAR FLORIDA, THE CARIBBEAN AND THE BAHAMAS

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ABSTRACT

Certain species of silversides and killifishes in the Florida Keys have generally been acknowledged to be distinct from peninsular Florida populations, with some (the Key Silverside *Menidia conchorum* and the Cuban Killifish *Fundulus grandis saguanus*) accorded distinct taxonomic status. However, morphological differences are slight and may represent differences typical of southern ends of clines. Our isozyme variation analyses do not support separate taxa for Keys populations of the Atherinid *M. conchorum* (probably synonymous with *M. peninsulae*) and the Cyprinodontids *F. grandis saguanus, F. similis, Lucania parva, Floridichthys carpio,* and *Cyprinodon variegatus*. This conclusion does not negate conclusions which may be drawn from morphological studies but such studies must weigh results against the seeming ecophenotypic plasticity of Atheriniform fishes. Species noted above and other Keys silversides and killifishes are threatened by development and human activity. Preservation of their habit and additional knowledge of their biology are needed. Relationships of Keys Atheriniform fishes to populations elsewhere in the Caribbean have also been investigated. Keys populations seem not to be related most closely to Yucatan populations as has been suggested, but rather to peninsular Florida populations. *Fundulus grandis* and *Cyprinodon variegatus* also occur in Cuba. These Cuban populations seem most closely related to those in the Florida Keys. Other Atheriniforms in the Caribbean such as *Chriopeoides* (Jamaica) and *Cubanichthys* (Cuba) appear to be much older relictual populations. Only three Cyprinodonts and three Atherinids occur in the Bahamas. The latter are widespread open water forms. The common Florida estuarine *Menidia* are absent in the Bahamas. Cyprinodonts include *Cyprinodon variegatus* which is presumably little different from *C. variegatus* of Florida, *C. laciniatus*, an endemic Bahamian form and *Rivulus marmoratus*, a widespread but secretive Caribbean species. Of note, is that even widely dispersed forms such as *Lucania parva, Fundulus grandis* and *F. heteroclitis* (or derivatives of it which even occur in Bermuda) are absent from the Bahamas.

INTRODUCTION

Atheriniform fishes of the families Atherinidae and Cyprinodontidae, silversides and killifishes, respectively, are common freshwater and estuarine fishes of the Atlantic coast of North America and the Caribbean region. Taxonomy, ecology, and zoogeography of these fishes are reasonably well known. In this paper we will summarize aspects of the systematics and geo-

graphical distribution of Florida populations of these fishes, with emphasis on the systematic status of populations in the Florida Keys. We examine:

1. systematic status of Florida Keys populations and their relationship to Florida peninsula populations
2. relationship of Florida Keys populations to Yucatan Peninsula populations
3. endemism in peninsular Florida and adjacent regions of the southern United States
4. relictual populations in the Caribbean region
5. Bahama populations

There is now a large body of systematic data and literature for North American atheriniform fishes based on both traditional morphological studies and more recent biochemical studies of isozyme and allozyme variation. The latter studies allow rather direct interpretation of allele frequencies in populations and relationships of populations.

Florida Keys populations of atheriniforms are a good focal point for this presentation because they have often been considered, on classical morphological grounds, to be taxa at either a species of subspecies level, because they exist in threatened, shallow water estuarine habitats, because they have been listed as species of special concern or as endangered species (Gilbert, 1978), and because of taxonomic affinity to other Florida and Caribbean populations. Understanding their relationship to other populations is important from systematic, zoogeographic, and conservation viewpoints.

Live-bearing killifishes (Family Poeciliidae; mollies, mosquitofishes) are not considered in this paper. In contrast to the killifishes (Cyprinodontidae), they have a more tropical distribution and may not have been as clearly influenced by events which have influenced killifish distributions in Florida and the Caribbean.

FLORIDA KEYS POPULATIONS

Morphological studies have suggested divergence of Florida Keys populations of marine and brackish water atheriniform fishes from peninsular Florida populations (Relyea, 1983, *Fundulus;* Relyea 1978, *Fundulus, Cyprinodon, Lucania, Poecilia;* Duggins, et al., 1983 a,b,c, 1986, 1989 and Duggins, 1980, *Cyprinodon, Lucania, Floridichthys, Fundulus, Menidia;* Robbins, 1969 and Gilbert, 1978, *Menidia*; Jordan 1884, *Cyprinodon).* The degree of divergence varies from species to species, and no firm conclusions regarding distinct Florida Keys species or subspecies has been possible, although populations of *Cyprinodon variegatus* from the Florida Keys have historically been allotted to *C. v. riverendi* (Jordan, 1884; Duggins et al., 1983a). In addition, Florida Keys and Cuban *Fundulus grandis* have been allocated to *F. g. saguanus* (see Rivas, 1948; Relyea, 1983; Duggins et al., 1989), and Keys populations of *Lucania parva* have been recognized as *L. venusta* (Jordan and Evermann, 1896). Morphological differences are seen as slight meristic variation and body proportion differences, traits which could be influenced by environmental conditions in Florida Keys. Low counts for meristic traits may indicate the southern end of clines.

In addition to morphological data, biochemical systematic data have now been published for the killifishes *Lucania parva* (Duggins et al., 1983b), *Floridichthys carpio* (Duggins et al., 1983c), *Cyprinodon variegatus* (Duggins et al., 1983a), *Fundulus grandis* (Duggins et al., 1989), and the Key silverside, *Menidia conchorum* Duggins et al., 1986). Unpublished data exist for the *Fundulus majalis - F. similis* species complex (Duggins et al., in prep.). Florida Keys populations of *Rivulus marmoratus, Fundulus confluentus,* and *Adinia xenica* have not been taxonomically evaluated in published reports, although Relyea (1965, unpublished Master's Thesis, Florida State University, Tallahassee) showed no statistically significant differences in Florida Keys *F. confluentus,* and Hastings and Yerger (1971) stated that there was little variation in *Adinia xenica* throughout its range, but published no data.

A species by species account of Florida Keys killifishes and silversides follows:

Atherinidae (silversides)

1. *Menidia conchorum* Hildebrand and Ginsburg (Key silverside) - *Menidia conchorum* was initially described as an endemic species from Key West (Hildebrand and Ginsburg, 1927). Duggins et al. (1986) have shown it to be more widely distributed in the middle and lower Keys than previously thought (Robbins, 1969; Johnson, 1975; Miller, 1976; Gilbert, 1978) and have shown it to be indistinguishable from the peninsular Florida silverside, *M. peninsulae*, on the basis of electrophoretic data for all allozymes. The morphological distinctiveness of *M. conchorum* may reflect ecophenotypic plasticity and not true genetic differences. However, we caution that this latter point remains to be demonstrated and the use of morphological data to delineate taxa such as *M. conchorum* remains a valid methodology. *Menidia conchorum* is considered endangered (Gilbert, 1978).

Cyprinodontidae (killifishes)

1. *Fundulus heteroclitus* (L.) - *Fundulus grandis* Baird and Girard species complex (mummichog and Gulf killifishes, resp.) - *Fundulus heteroclitus*, the common mummichog of the Atlantic coast, is a temperate species which extends into NE Florida (Relyea, 1983). It is replaced southward from NE Florida along the Atlantic coast by *F. grandis*, the Gulf killifish, which also occurs in the Florida Keys and throughout the Gulf of Mexico into NE Mexico. An allopatric form occurs in Yucatan (Hubbs, 1936; Miller, 1955, 1966; Relyea, 1983). Relyea (1983) placed Florida Keys populations with *F. g. saguanus*, a Cuban subspecies described by Rivas (1948), on the basis of morphological traits. Duggins et al. (1989), using electrophoretic techniques for isozyme isolation and allele frequency determination, could not validate the distinctiveness of Florida Keys populations from peninsular Florida populations. This parallels the situation for *Menidia conchorum* (above). Cuban populations, the nominal *F. g. saguanus*, have not been examined using biochemical techniques. Florida Keys populations of *F. grandis* are considered a "species of special concern" (Relyea, 1978).

2. *Fundulus majalis* (Walbaum) - *Fundulus similis* Baird and Girard species complex (striped and long nosed killifishes, resp.) - Members of this species complex have an overall distribution similar to that of the *F. heteroclitus* - *F. grandis* complex (Relyea, 1983). The temperate form *F. majalis*, is replaced in NE Florida by the southern form *F. similis*, in a complex pattern of hybridization or introgression. There is no evident sympatry as in *F. heteroclitus* and *F. grandis*. An allopatric population, nominally *F. persimilis*, occurs in Yucatan (Miller, 1955, 1966; Relyea, 1983). There is no Cuban population. The population in the Florida Keys is distinct on the basis of morphological traits, paralleling again *F. grandis* and *Menidia conchorum* (Relyea, 1983). Duggins et al. (in prep.) have biochemical data that do not indicate any significant differences for Florida Keys populations from populations in the Florida peninsula, again paralleling the above noted species.

3. *Cyprinodon variegatus* Lacepede (pupfish) - Duggins et al. (1983a) presented biochemical data for Florida populations of this wide ranging pupfish (see account of Florida endemic populations which follows), including Florida Keys populations which have been allotted, along with Cuban specimens, to *C. v. riverendi* (Jordan, 1884). Biochemical data for Keys populations suggest some divergence from Florida peninsula populations, but to recognize distinct taxa in this very variable species is probably not justified on the basis of slight variation.

4. *Lucania parva* (Baird) (rainwater killifish) - Duggins (1980) suggested that Florida Keys populations of the rainwater killifish were morphologically different from peninsular Florida populations but not sufficiently so to warrant taxonomic recognition. Earlier authors (see Jordan and Evermann, 1896) had considered Florida Keys populations to be distinct species, *L. venusta*. Duggins et al. (1983b) analyzed electrophoretic data for *L. parva* from Atlantic and Gulf of Mexico coasts of Florida, the Florida Keys, and Yucatan and could show no variation of significance. As with the other atheriniform fishes noted above, slight morphological differences can be shown for Keys populations, but biochemical analyses fail to validate such differences.

Again, morphological traits may reflect phenotypic plasticity.

5. *Floridichthys carpio* (Gunther) (Gold spotted killifish) - Duggins et al. (1983c) analyzed electrophoretic data for populations throughout the range of *F. carpio* (Florida Atlantic and Gulf of Mexico coasts and Florida Keys), and for the Yucatan population, nominally *F. polyommus*. No differences could be shown for Florida Keys populations relative to peninsular Florida populations (see Florida Keys - Yucatan discussion of *F. polyommus* which follows). Morphological differences for Keys populations are also slight, unlike the situation for aforementioned species. *Floridichthys carpio* is seemingly a south Florida form without temperate relationships.

6. Other species - Three other species of estuarine killifishes occur in the Florida Keys, *Rivulus marmoratus* (Poey), *Fundulus confluentus* (Goode and Bean) and *Adinia xenica* (Jordan and Gilbert). No biochemical systematic data are available for these species. *Rivulus marmoratus* is a tropical species which is widespread in south Florida and the Caribbean (Taylor, 1990). Systematic study of *Rivulus* is needed. *Fundulus confluentus* has been examined from a morphological standpoint (Relyea, 1965, unpublished Masters Thesis, Florida State University) and no significant differences could be shown for Florida Keys populations in comparison to peninsular Florida populations. Hastings and Yerger (1971) stated that there was little variation in morphological features of *Adinia xenica* throughout its range (extreme south Florida, Florida Keys and Gulf of Mexico to southern Texas). Of the species noted above, only *Fundulus confluentus* ranges very far northward on the Atlantic coast (Chesapeake Bay). *Rivulus* seems to be restricted to southern Florida, and *Adinia* does not range north of Miami. *Adinia* and *F. confluentus* occur throughout the Gulf of Mexico to the southern Texas coast, but neither occurs in Yucatan. *Rivulus* does not occur in the northern Gulf, but is common in Yucatan. It is striking that the silverside and killifishes considered earlier as possibly having unique taxa in the Florida Keys also have related populations or taxa in Yucatan, whereas *Adinia* and *F. confluentus*, for which there is no indication of differentiation in the Florida Keys, lack Yucatan populations.

FLORIDA KEYS -YUCATAN RELATIONSHIPS

Populations of *Menidia (M. colei* and undescribed forms), *Floridichthys, Lucania parva, Cyprinodon variegatus* and *Fundulus* occur in Yucatan. A summary follows:

1. *Menidia* - The *Menidia* populations of Yucatan (*M. colei*; undescribed forms) seem to not be especially closely related on basis of biochemical data to *Menidia conchorum* of the Florida Keys (Duggins et al., 1986), which as noted earlier, is probably a synonym of *M. peninsulae* of Florida and the Gulf of Mexico. Morphological variation in *Menidia* is considerable and likely represents environmental effects on the genetic expression of those traits, rendering morphological data difficult to interpret (see Duggins et al., 1986). Biochemical data suggest, weakly perhaps, a relationship of Yucatan to western Gulf of Mexico populations (Duggins et al., 1986) This suggestion seems to apply to the fishes treated in this section as well.

2. *Floridichthys* - An allopatric population of *Floridichthys, F. polyommus* occurs in Yucatan (Duggins et al., 1983c; Hubbs, 1936). *Floridichthys carpio barbouri* and *F. c. polyommus* were originally recognized by Hubbs (1936) as distinct Yucatan forms, but Duggins et al. (1983c) show that Yucatan forms all could be allotted to one distinct species, *F. polyommus*. Morphological and biochemical data support this allocation. The relationships of *F. polyommus* can only be with *F. carpio* of Florida although this does not imply a Florida Keys - Yucatan affinity or dispersal. *Floridichthys polyommus* could have been derived from western Gulf of Mexico populations that may have existed during some interglacial period, or even more recently. In fact, the type locality of *F. carpio*, as *Cyprinodon mydrus* (Hubbs, 1926) is Pensacola, Florida, a locality far to the west of currently extant *F. carpio* populations (Apalachicola, Florida area). A restriction of the range of *F. carpio* may have occurred on very recent times.

3. *Lucania parva* - this small killifish seems to have the most uniform gene pool throughout its range of all the killifishes considered here.

Yucatan populations are seemingly conspecific with other populations in the Gulf of Mexico and Florida, including the Florida Keys, and show little morphological and biochemical divergence from those populations, despite being allopatric (Duggins et al., 1983b).

4. *Cyprinodon variegatus* - Yucatan populations of this species have been relegated to subspecific status as *C. v. artifrons* (Hubbs, 1936). Morphological and biochemical studies are needed to clarify the status of this taxon. The distinctiveness of the Yucatan populations from those in Florida, especially the Keys, has not been determined. There are certainly pigmentary differences. Yucatan populations may be closely related to populations in the western Gulf of Mexico. Other species of *Cyprinodon* in Yucatan are beyond the scope of this paper (see Humphries and Miller, 1981).

5. *Fundulus heteroclitus* - *F. grandis* species complex - This species group is represented in Yucatan by the allopatric form, *F. grandissimus* (Relyea, 1983; Miller, 1955, 1966; Hubbs, 1936). Morphological studies indicate that this is a valid species (Hubbs, 1936; Relyea, 1983), but no biochemical analysis is available. Of note is that meristic and morphometric data for *F. grandis* populations in the Florida Keys and *F. g. saguanus* of Cuba suggest more strongly than for any other killifishes an affinity for *F. grandissimus* to western Gulf of Mexico populations. It is this species complex which sets the hypothesis of a western Gulf - Yucatan corridor of dispersal.

6. *Fundulus majalis* - *F. similis* species complex - *Fundulus persimilis* Miller is the allopatric Yucatan representative of this species complex (Miller, 1955; Relyea, 1983). No biochemical data are available to compare this form to populations in south Florida and the western Gulf of Mexico. On a morphological basis, this species appears to be a valid taxon not closely related to the Florida Keys *F. similis* form, and as for *F. grandissimus* (considered above), is seemingly most closely related to western Gulf of Mexico *F. similis*.

7. *Garmanella pulchra* Hubbs - *Garmanella* is a monotypic genus with the only species, *G. pulchra*, being restricted to the Yucatan Peninsula. Suggestions have been made that *G. pulchra* is related to *Floridichthys* and/or *Jordanella*. These assertions have not been tested by either morphological or biochemical studies.

ENDEMISM IN THE FLORIDA PENINSULA

Several taxa of killifishes and one silverside are endemic to the freshwaters of the Florida peninsula and/or nearby coastal plain regions of Georgia and Alabama. One species noted earlier, *Floridichthys carpio*, is the only endemic brackish water species of killifishes distributed in the Florida peninsula. The following is an account of endemic freshwater forms.

1. *Menidia beryllina atrimentis* - The taxonomic status of this nominal subspecies of silverside remains to be truly tested by modern systematic techniques. Given the morphological variability within *Menidia*, any subspecific designation must be viewed with caution. *Menidia b. atrimentis* occurs in the same central Florida lakes in which a nominal subspecies of *Cyprinodon variegatus, C. v. hubbsi*, occurs, and was presumably isolated by the same geological events that isolated those pupfish (see Gilbert, 1987). Most of these lakes (Dora, Harris, Griffin, Eustis, Yale, Weir, and nearby smaller ones) have become extremely eutrophic in recent years, have been exposed to herbicides for aquatic weed control, and have experienced introduction of exotic fish species, all factors which pose a threat to the endemic fishes.

2. *Cyprinodon variegatus hubbsi* (or *C. hubbsi*) - Carr (1936) described this unique taxon from Lake Eustis in central Florida. It is now known as well from Lakes Dora, Harris, Griffin, Weir, Yale and Silver (Johnson and Snelson, 1978). The validity of this form as a subspecies or distinct species related to the more brackish water *C. variegatus* has long been debated on morphological grounds, but without resolution. Biochemical data have not clarified the issue, but do suggest that *"hubbsi"* is not markedly distinct from *C. variegatus* and

probably does not deserve specific recognition (Duggins et al., 1983a).

3. *Jordanella floridae* Goode and Bean - The Florida flagfish is found throughout the Florida peninsula to about the Ochlockonee River in the panhandle in fresh water swamps, ditches, spring runs, and ponds. Its relationship to other killifishes is unclear (Gilbert, 1987). It has probably been isolated in the Florida peninsula since some early glacial period, or perhaps even pre-Pleistocene times.

4. *Lucania goodei* Jordan - The blue fin killifish is found throughout the Florida peninsula in ecological circumstances much like that of *Jordanella floridae*. It ranges slightly farther west than *Jordanella*, and there is a record from the Choctawahatchee drainage is southern Alabama (Smith-Vaniz, 1968). There are also records from coastal Georgia (Dahlberg, 1975). Duggins et al. (1983b) showed little variation in this species for biochemical traits through its range, and clearly demonstrated it is distinct from the brackish water *L. parva* its closest relative. Presumed relatives elsewhere of both *L. goodei* and *L. parva* are the Caribbean insular endemics *Cubanichthys cubensis* (Cuba) and *Chriopeoides pengelleyi* (Jamaica).

5. *Fundulus seminolis* Girard - The seminole killifish is an inhabitant of lakes, rivers, and spring runs throughout the Florida peninsula and westward to the Panama City area (Relyea, 1975). Its relationships within the genus *Fundulus* are unclear. They may rest with brackish water *F. majalis* - *F. similis* or with more northern forms such as *F. diaphanus* or *F. waccamensis*. Unpublished data for meristic features suggest little variation within the species. Biochemical data are not available.

6. Other Florida species - *Fundulus chrysotus, F. cingulatus*, members of the *F. lineolatus* species complex, especially *F. lineolatus*, and *Leptolucania ommata*, have distributions throughout much of the Florida peninsula. *Leptolucania ommata* does not range as far southward (to Osceola Co.) as others, which occur through the Everglades. All three range into the coastal plain of Georgia and westward along the Gulf coastal plain. None seems to be related to forms anywhere in the Caribbean. Three other killifishes, two of them brackish water species, occur in Florida. These are the previously mentioned *Rivulus marmoratus* of south Florida and the Caribbean, a western Gulf of Mexico species, *Fundulus jenkinsi*, which ranges into the panhandle near Pensacola, and the freshwater form *F. olivaceus* in the panhandle from the Apalachicola River westward (Relyea, 1975). Another form, the nominal *F. escambiae*, a member of the aforementioned *F. lineolatus* complex, occupies the Florida panhandle eastward to the Suwannee River drainage and is replaced eastward and southward by *F. lineolatus* (Wiley, 1977). Biochemical studies of the *"lineolatus"* complex are needed.

CARIBBEAN INSULAR RELICTS

Dispersal of killifishes to Caribbean Islands (see Rosen, 1975), probably during Pleistocene glaciations has led to several relictual populations. Most notable of these are *Cubanichthys cubensis* of Cuba and *Chriopeoides pengelleyi* of Jamaica, both of which, as noted earlier, are seemingly related to *Lucania parva* of the Atlantic and Gulf of Mexico coasts, and to *L. goodei* of Florida.

Populations of *Fundulus grandis* nominally *F. g. saguanus* and *Cyprinodon variegatus* nominally *C. v. riverendi*, occur in Cuba. Additional populations of *Cyprinodon, C. jamaicensis, C. bondi*, and *C. dearborni* occur in Jamaica, Haiti, and the Dutch West Indies, respectively. These *Fundulus* and *Cyprinodon* populations seem to be not as divergent from related Florida populations as *Cubanichthys* and *Chriopeoides*. Different isolation times are indicated. *Rivulus marmoratus* is found on islands throughout the Caribbean, and its distribution can not be viewed as relictual. It apparently has some way of crossing wide expanses of ocean.

As a final note in this section, atherinids of the inshore genus *Menidia*, the silversides, are unknown from Caribbean islands.

BAHAMA KILLIFISHES

Three species of killifishes and one mosquitofish (Poeciliidae, *Gambusia manni*) are

known to occur in the Bahamas; no *Menidia* silversides are known there. Three reef dwelling or pelagic silversides, including the wide ranging *Atherinomorus stipes*, are found in the Bahamas as well as elsewhere in the Caribbean and Florida (Bohlke and Chaplin, 1968). The cyprinodontids are *Cyprinodon variegatus*, which occurs throughout the Bahamas in ponds, ditches and limestone solution holes, *C. laciniatus*, an endemic species on New Providence Island, and wide ranging and previously considered *Rivulus marmoratus*. *Cyprinodon baconi* Breder from Andros Island was placed in the synonymy of *C. variegatus* by Miller (1962) (also see Bohlke and Chaplin, 1968). Additional analysis of the Bahamian *Cyprinodon* is needed. As noted above, only one poeciliid, the Bahamian endemic *Gambusia manni*, is known from the Bahamas.

What is most striking about the Bahamas is the absence of *Fundulus*, *Floridichthys*, *Lucania*, and *Menidia* in habitats seemingly identical to those which these fishes inhabit in peninsular Florida and the Florida Keys, suggesting either lack of dispersal of these forms or some habitat features or competitors which exclude them. That *Cyprinodon*, the most widespread and seemingly genetically flexible temperate killifish, and *Rivulus*, the wide ranging Caribbean form are the successful colonizers of the Bahamas is perhaps not unexpected. A final note is that the extremely common Florida estuarine poeciliid, the sail fin molly, *Poecilia latipinna*, is absent from the Bahamas.

DISCUSSION

Populations of killifishes (Cyprinodontidae) and silversides (Atherinidae) in the Florida Keys, with the exception of the tropical *Rivulus marmoratus*, have evidently been derived from temperate zone forms found northward in the Florida peninsula and along the Gulf of Mexico and Atlantic coasts of the United States. Morphological studies have suggested that Florida Keys populations of these fishes may have differentiated from peninsula Florida populations at a species or subspecies level. Species with a more restricted southward distribution or limited temperate populations, *Floridichthys carpio*, *Fundulus confluentus* and *Adinia xenica*, do not show this divergence in the Florida Keys. Biochemical studies, however, fail to support the distinctiveness of these Florida Keys populations and raise the possibility that morphological traits may be influenced by environmental factors such as temperature, substrate, and salinity. These morphological traits often seem to represent southern extremes of clinal variation. Florida Keys populations may not represent distinct gene pools, an important consideration given that all are classified as endangered or as species of special concern (Gilbert, 1978).

In addition, Keys populations seem not to be especially closely related to congeneric Yucatan populations. Morphological and biochemical data, where available, both support this. Only *Lucania parva* does not show considerable divergence for Yucatan populations from Keys populations, but even for *L. parva*, relationships, as with other Keys species with Yucatan relatives, appear to be with western Gulf of Mexico populations. This argues for an origin of Yucatan populations as relicts left behind as populations extended ranges northward behind retreating glacially determined conditions, as opposed to oceanic dispersal or land bridge connections from the Florida Keys to Yucatan (see Rosen, 1975). The lack of differentiation of *L. parva* in Yucatan, however, could be due to attachment of eggs to floating sea grasses such as *Syringodium*. It is striking that *L. parva* the smallest species of killifish considered here, and presumably the least capable of crossing ocean barriers, is the species with the least population differentiation. In summary, Florida Keys populations are southernmost populations of temperate killifishes in the Florida peninsula to the north, and Yucatan populations are allopatric forms mostly differentiated at a species or subspecies level, probably derived from the western Gulf of Mexico, and not closely related to Florida Keys populations.

Other Caribbean populations are certainly glacial relicts. This is best seen with *Cyprinodon* populations in Jamaica, Haiti, Cuba, and the Dutch West Indies. One *Fundulus*, *F. grandis saguanus*, occurs in Cuba. These Cuban populations are recent relicts and are little, if any, differentiated from Florida Keys populations. However, the relicts *Cubanichthys cubensis* of Cuba and *Chriopeoides pengelleyi* of Jamaica, are most closely related to the genus *Lucania* of Florida and

the Atlantic and the Gulf coasts, and probably represent rather early relicts or even pre-Pleistocene relicts. *Lucania goodei* itself is probably an early Pleistocene glacial endemic to Florida freshwaters. The issue of endemism in peninsular Florida is related to this. Relyea et al. (1976) argued that extensive troglobitic crustacean cave fauna of Florida (and Cuba) and the endemic killifishes of Florida (*Jordanella, Fundulus seminolis, Lucania*) survived cold temperate conditions dictated by the northern glaciers in constant temperature subterranean waters or their spring outflows. *Garmanella* of Yucatan may be an early Pleistocene relict as well. This isolation process has continued with more recent glaciations hence *Cyprinodon* populations in Yucatan, Cuba, Caribbean Islands, the Bahamas, and central Florida lakes, *Fundulus* in Cuba and Yucatan, and *Lucania, Floridichthys* and *Menidia* in Yucatan. With four clearly defined glacial periods, each followed by glacial retreat and population movements of fishes compressed toward the tropics, there have surely been at least four major possible periods of isolation of these atheriniform fishes. Some such as *Cubanichthys, Chriopeoides, Garmanella*, and *Jordanella* seem to be very early isolations as there great differences in morphology from any other extant forms. *Lucania goodei* may be more recent. Forms such as the various *Cyprinodon variegatus* related populations may be very recent. The sequence of isolation of various populations may be impossible to determine.

What is perhaps most striking is the absence of more killifish and silverside populations in the Caribbean. The fact that there are quite a few killifish and silverside taxa in Yucatan but not many in insular situations points markedly to lack of ability of atheriniform fishes to cross ocean barriers. They hug shorelines. Even the very common *Menidia, Lucania, Floridichthys*, and mollies, *Poecilia*, of Florida shorelines are absent in Cuba and the Bahamas, and the latter islands lack even the one *Fundulus* species found in Cuba. The Bahamas, especially, are an enigma given the similarity of mangrove and salt marsh habitat to that in Florida in which atheriniforms abound. Habitat that would be teeming with *Menidia, Lucania, Fundulus*, and *Floridichthys*, and even the less common *Adinia*, is simply devoid of fishes in the Bahamas.

We have noted small schools of immature parrotfishes (Scaridae) in killifish-like situations around mangrove prop roots in the Bahamas, however. Obviously, the oceanic gap between peninsular Florida and the Bahamas is a major barrier to dispersal of these inshore killifishes and silversides. Even *Lucania parva*, which as noted earlier may maintain gene flow between isolated populations by possibly attaching eggs to floating seagrasses such as *Syringodium*, is absent from the Bahamas. The only killifishes present are *Cyprinodon variegatus*, the endemic *C. laciniatus*, and *Rivulus marmoratus*. The latter is clearly capable of island hopping and crossing ocean gaps. How it does so is unknown. However some individuals are synchronous hermaphrodites capable of self fertilization, a probable aid in colonization. *Rivulus* can also tolerate extremes of water quality and even resides in often foul land crab burrows (Taylor, 1990). *Cyprinodon variegatus* is also a successful colonizer with a widespread distribution. Perhaps *Rivulus* and *Cyprinodon* moved from peninsular Florida to the Keys to Cuba, or *Rivulus* may have inverted that route, and then up through the Bahama chain. The absence of other killifishes, silversides, and poeciliids in the Bahamas suggests such a route. There are no populations to the north to colonize the Bahamas as there are to the north of the Florida Keys, Cuba and Yucatan, and it is only *Rivulus, Cyprinodon*, and *Fundulus (F. grandis saguanus)* which are present to the south in Cuba, and the latter has not gained access to the Bahamas. The Bahamas have not been on a north to south corridor for range movements in the Pleistocene, but have been on south to north path for species which were successful in reaching and surviving in Cuba during some glacial period and then moving northward again with retreat of glacial conditions. *Cyprinodon laciniatus* may represent an earlier south to north movement. Its very restricted occurrence on the small island of New Providence, however, is really unexplainable.

Killifishes and silversides have dispersed in tantalizing and limited fashion to Caribbean islands, Yucatan, the Bahamas, and the Florida Keys, and have left relictual populations of varying age. They do not cross oceanic gaps of any great extent, or even moderate extent, and may be

only moderately successful colonizers should they gain access to islands. *Rivulus* and *Cyprinodon* are the only clearly successful colonizers. All this said, it must be noted in closing that two species clearly derived from *Fundulus heteroclitus*, nominally *F. rhizophorae* and *F. bermudae*, occur in Bermuda. Some mechanism of transoceanic transport, perhaps drifting in the Gulf Stream, must have existed. Why *Fundulus* do not occur in what appear to be the far more accessible Bahamas, or why there are not more *Fundulus* and other species of killifishes in Cuba is still a mystery.

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