

Premating Isolating Mechanisms Among Three Species of the *Rana pipiens* Complex in Texas and Southern Oklahoma

DAVID M. HILLIS

Prior tests of interfertility among 3 partly sympatric species of the *Rana pipiens* complex (*R. berlandieri*, *R. blairi*, and *R. sphenoccephala*) have indicated poor development of postmating reproductive isolation. However, hybrids are uncommon in sympatric populations, so premating isolation must exist. Among the species studied, temporal isolation predominates. In areas of tri-sympatry, the breeding seasons of all three species are staggered, whereas in allopatric areas the breeding seasons are expanded. Habitat isolation and ethological isolation also appear to be important, at least among some sympatric combinations of leopard frogs in Texas. Hybrids are presumably more poorly adapted to either parental habitat than are nonhybrids; thus postmating selection for conspecific mating through hybrid inferiority is at least partly responsible for the reinforcement of breeding season displacement in sympatry.

IN recent years North American leopard frogs (*Rana pipiens* complex) have come under thorough systematic scrutiny, and the work of a number of investigators (Post and Pettus, 1966; Mecham, 1968; Littlejohn and Oldham, 1968; Platz, 1972; Pace, 1974) has demonstrated that the *R. pipiens* complex consists of many distinct, generally parapatric, species. The studies of these and other workers have led to the description of several new species (Sanders, 1973; Mecham et al., 1973; Frost and Bagnara, 1976; Platz and Mecham, 1979), and additional species in this complex remain to be described—especially in Middle America and the southwestern United States.

After morphologically, auditorially and electrophoretically distinct species became recognized, comprehensive distributional studies of the *R. pipiens* complex located a number of zones of sympatry between various species of leopard frogs, with very little natural hybridization (Post and Pettus, 1967; Mecham, 1968; Brown and Brown, 1972; Platz, 1972; Platz and Platz, 1973; Dunlap and Kruse, 1976; Frost and Bagnara, 1977a, b; Lynch, 1978). Whereas only infrequent hybridization of sympatric species of leopard frogs has been reported in the field, laboratory studies have shown high degrees of interspecific genetic compatibility within this group (Moore, 1946a, b, 1947, 1950, 1966, 1967a, b; Mecham, 1969; Frost and Bagnara, 1976, 1977b). These studies have indicated that postmating isolating mechanisms are poorly

developed within the *R. pipiens* complex, and that relatively well developed premating (= anti-mating of Fouquette, 1960) isolating mechanisms must therefore exist in order to maintain the low degree of natural hybridization among leopard frogs.

Littlejohn and Oldham (1968) presented evidence of differentiation in mating calls of species in the *R. pipiens* complex in Texas. Little subsequent work on premating isolating mechanisms of the Texas species of leopard frogs has appeared. Elsewhere studies of the *R. pipiens* complex have failed to agree on the role of various premating isolating mechanisms. The present investigation was undertaken to study premating isolating mechanisms involved in sympatric combinations of *Rana berlandieri*, *Rana blairi* and *Rana sphenoccephala* (= *R. utricularia* of Pace, 1974) in Texas and southern Oklahoma.

METHODS

Seven general areas were studied; in each of these areas observations were made at a number of different sites. Allopatric populations of each of the three species were studied—*R. berlandieri* in southern Llano and northern Gillespie counties, Texas; *R. blairi* in central Oklahoma and in north central Texas; and *R. sphenoccephala* in eastern Texas. Sympatric populations of *R. berlandieri* and *R. blairi* were investigated in Brown, Coleman and Comanche

counties, Texas; *R. berlandieri* and *R. sphenoccephala* were studied in sympatry primarily in McLennan and Falls counties, Texas; and observations were made on sympatric populations of *R. blairi* and *R. sphenoccephala* in southern Oklahoma, from Cotton County to Marshall County, inclusive. Observations were also carried out in an area in central Texas including parts of Bosque, Johnson, McLennan and Somervell counties in which all three of these species of leopard frogs occur.

In addition to field observations in the above study areas, leopard frogs were collected throughout Texas and southern Oklahoma to define the ranges of these three species and the extent of the zones of sympatry. Preserved specimens were examined from the collections of the University of Kansas Museum of Natural History, Strecker Museum of Baylor University, Texas Natural History collection of the University of Texas at Austin, and the personal collections of Bryce C. Brown and Ottys Sanders. Locality data were recorded and reproductive condition was noted. Either field notes concerning reproductive activity or obvious signs of reproductive condition in preserved specimens (females with well developed eggs and males with extended vocal sacs) were used to determine reproductive activity. No reproductive dates derived from preserved specimens were considered valid unless supported by field observations.

Observations for this study were carried out from August 1976 until March 1980. Observations were made in the field during every month of the year in all study areas except for the Oklahoma study sites and the *R. berlandieri*-*R. blairi* sympatric zone. The Oklahoma study sites were studied primarily during the summer months of 1978, and were visited briefly during the springs of 1978, 1979 and 1980. The zone of sympatry between *R. berlandieri* and *R. blairi* was visited sporadically from April 1977 until November 1978, but during each season of the year.

During field observations all evidence of reproductive activity of leopard frogs was noted. Evidence considered valid for the establishment of "reproductive activity" included the presence of egg masses, amplexus, or recently hatched tadpoles. When any doubt existed as to identity of eggs or tadpoles, a sample was raised in the laboratory until positive identification became possible. Characteristics of tadpoles noted by

Korky (1978—*R. blairi*) and Hillis (in press—*R. berlandieri* and *R. sphenoccephala*) were used in identification; tadpoles were often raised to metamorphosis to check identifications.

At each locality where leopard frogs were found, notes were made concerning specific habitat parameters. These notes included references to vegetation type, soil type, terrain, relative permanence of water, type of water body, water temperature, degree of human interference, and any other distinguishing characteristics.

GEOGRAPHIC DISTRIBUTION

The ranges of *R. berlandieri*, *R. blairi*, and *R. sphenoccephala* in the south central United States, as determined on the basis of personal sight and collection records, examined museum specimens, and selected literature records, are shown in Fig. 1. Included as records for *R. berlandieri* are specimens from Trans-Pecos Texas, which may represent an undescribed form. In addition, specimens of leopard frogs from the type locality of *R. berlandieri* in southern-most Texas appear to be morphologically distinct from what is referred to herein as *R. berlandieri* throughout the rest of Texas; however, pending further study, the name *R. berlandieri* is used as indicated in Fig. 1. I consider all of the Mexican "subspecies" of *R. berlandieri* to be distinct species, as several bear little morphological, ecological or ethological resemblance, and since no contact or intergradation has been reported among the various forms. Thus *R. berlandieri forreri*, as used by Frost and Bagnara (1977b) following Sanders and Smith (1971), becomes *R. forreri*, and *R. berlandieri brownorum* Sanders (1973) becomes *R. brownorum*.

Geographic isolation is highly important in the *R. pipiens* complex as a whole since the ranges of leopard frogs are roughly parapatric and the areas of sympatry are comparatively small. The largest area of sympatry of leopard frogs previously reported was that of Frost and Bagnara (1977b)—they found *R. magnaocularis* and *R. forreri* in sympatry throughout a coastal strip 15–80 km in width, extending from southern Sonora to northern Nayarit in Mexico. Several zones of sympatry between various species of leopard frogs found in this study cover considerably more area than the literature (Littlejohn and Oldham, 1968; Pace, 1974; Conant, 1975) indicates, and represent the largest areas

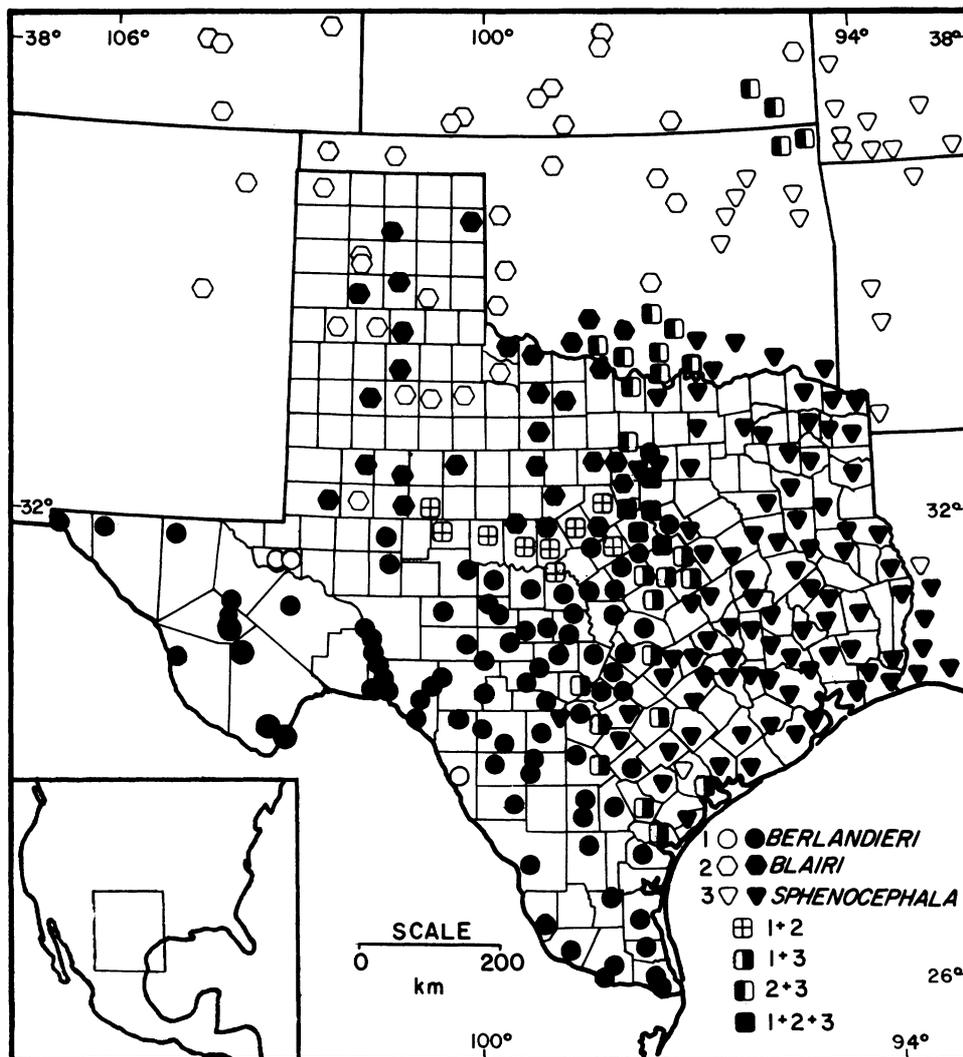


Fig. 1. Distributions of *Rana berlandieri*, *Rana blairi*, and *Rana sphenoccephala* in the south central United States. Solid symbols represent examined specimens, open symbols represent selected literature records.

of sympatry yet reported for members of the *R. pipiens* complex (from this group I exclude the highly differentiated *R. palustris*). The zone of sympatry between *R. blairi* and *R. sphenoccephala* is at least 140 km wide in southern Oklahoma, and extends south of the Texas/Oklahoma border 250 km to northwestern McLennan County, Texas, and north to southeastern Kansas (Fig. 1). This extends the known range of *R. sphenoccephala* as reported by Pace (1974) to the west in Oklahoma by approximately 140 km, and the range of *R. blairi* as reported by Littlejohn and Oldham (1968),

Mecham et al. (1973), and Pace (1974) by approximately 100 km to the southeast. Fig. 1 contains many new county records, and includes range extensions for all three species of leopard frogs in Texas.

The presence of *R. sphenoccephala* as far west as Cotton County, Oklahoma (Fig. 1) raises question to the interpretations of Pace (1974) regarding Bragg's (1949, 1950a, 1950b, 1950c) observations of leopard frogs in Oklahoma. Pace (1974) referred Bragg's "*R. berlandieri*" to *R. blairi* more often than is justifiable, since Bragg must have made observations of *R.*

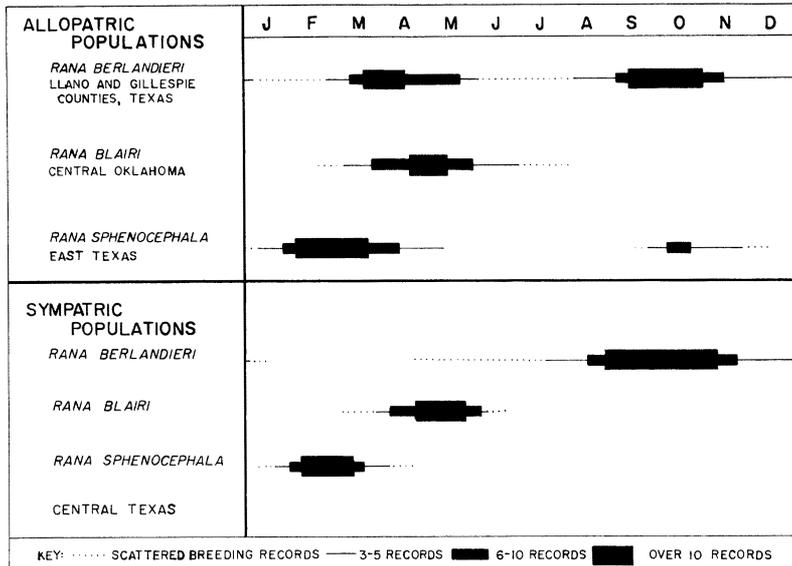


Fig. 2. Breeding records of sympatric and allopatric populations of three species of leopard frogs.

sphenocephala in sympatry with *R. blairi* in an area much larger than considered by Pace. As a result of this mistake, the breeding season reported for *R. blairi* by Pace (1974), as taken from Bragg (1950a), actually represents the compilation of breeding records for *R. blairi* and *R. sphenocephala* in Oklahoma. In addition, the presence of *R. pipiens* in Oklahoma (Pace, 1974) needs to be verified. It is probable that the two species that Bragg (1950c) recorded in Stephens County were not *R. pipiens* and *R. blairi* as interpreted by Pace (1974), but *R. sphenocephala* and *R. blairi* (I have found *R. sphenocephala* in Cotton, Jefferson, Carter and Garvin counties, which nearly surround Stephens County). A single specimen of *R. pipiens* does exist, however, from Caddo County, Oklahoma (University of Michigan Museum of Zoology 68754, not examined—identified in Pace, 1974).

REPRODUCTIVE ISOLATION

Temporal (seasonal) isolation.—Temporal isolation is probably the single most important isolating mechanism among sympatric leopard frogs in central Texas (Fig. 2). In areas of sympatry, there is a displacement of breeding seasons, with breeding restricted to late winter and early spring for *R. sphenocephala*, to late spring and early summer for *R. blairi*, and to fall and

early winter for *R. berlandieri*. However, allopatric populations are not so restricted. Allopatric populations of *R. berlandieri* (in this study, in southern Llano and northern Gillespie counties, Texas) have a split breeding season, breeding both in the spring as well as in the fall. *R. sphenocephala* in east Texas, in the absence of any other species of leopard frogs, breeds during the fall (although to a lesser extent) as well as in late winter and early spring. *R. blairi* in allopatry also appears to have a somewhat expanded breeding season compared to populations in sympatry with other leopard frogs. Although the breeding seasons of these three frogs in sympatry do allow for some minor overlap, this is limited to years of meteorological extremes. Even in such years, the majority of breeding is likely to be carried out without interspecific competition.

The partitioning of breeding seasons of sympatric leopard frogs may at first seem discordant to statements in the literature that record two species calling together at the same place and time (Littlejohn and Oldham, 1968; Pace, 1974). However, in many species of leopard frogs males call well outside the breeding season (see, for example, the records of calling leopard frogs versus the egg deposition dates recorded by Blair, 1961). It was for this reason that dates of calling leopard frogs, without evidence of breeding activity, were not used to

define breeding seasons in this study. It is even possible that calling males of one species may stimulate males of another species to call, without stimulating breeding activity. This is especially likely since some leopard frog calls have been associated with male territoriality behavior (Gamb and Littlejohn, 1979). Or, alternatively, the converse may be true—the calling of one species may depress reproductive activity in another species, and thus serve as an additional isolating mechanism.

Sage and Selander (1979) stated that “there apparently is no significant temporal separation of reproductive activities [of *R. berlandieri* and *R. sphenoccephala*] in central Texas; both species breed from September through February (Blair, 1961; R. D. Sage, pers. observ.).” This statement is, in fact, contradictory to the findings of Blair (1961). Blair reported reproductive activities of “*R. pipiens*” (within the zone of sympatry of *R. berlandieri* and *R. sphenoccephala*); he reported 6 egg masses in February, 7 in April, 2 in July, 4 in August and 4 in September. A significant portion of the breeding seasons of both species occurs outside of the months reported by Sage and Selander (1979); in naturally sympatric populations the breeding seasons of the two species are staggered.

Platz (1972) believed that temporal isolation was not important in the isolation of *R. berlandieri* from *R. blairi* in Mitchell and Coke counties, Texas. Platz stated that he found gravid females of both species throughout the summer, although he also stated that *R. berlandieri* may begin breeding earlier in the spring than does *R. blairi*. Breeding seasons of leopard frogs cannot be defined simply on the basis of the presence of gravid females, however, since gravid females can be found well before the start of the breeding season. The breeding seasons of these two species in sympatry would not have to be greatly modified from those of the allopatric populations in order to achieve temporal isolation (Fig. 2). Therefore, it is likely that *R. berlandieri* breeds both before and after (but not along with) *R. blairi* where these two species are sympatric, which may have led to Platz's (1972) conclusion. Among other sympatric pairs of leopard frogs, temporal isolation has also been considered an important isolating mechanism. Frost and Bagnara (1977b) reported temporal isolation to be the primary mechanism of isolation between *R. magnaocularis* and *R. forreri* in western Mexico. Post and Pettus (1967) believed that temporal isolation was at

least partially responsible for isolating *R. blairi* (their DF complex) from *R. pipiens* (their CF complex) in Colorado, and Dunlap and Kruse (1976) reached similar conclusions for these two species in sympatry in South Dakota. Lynch (1978) disagreed with both of these latter papers, since he found *R. pipiens* and *R. blairi* calling together in April, May, and June in Nebraska. Pettus and Post (1969) reported that while naturally sympatric populations of *R. pipiens* and *R. blairi* were isolated by non-overlapping breeding seasons, populations of these two species which became sympatric due to human construction of new breeding habitat were not so isolated. Studies concerning the level of “natural hybridization” or concurrent breeding among sympatric leopard frogs should take into account the possibility of recent (human induced) contact. This type of sympatry may explain the relatively high levels of hybridization between *R. berlandieri* and *R. sphenoccephala* reported by Salthe (1969) at a locality near Luling, Texas. Sage and Selander (1979) also reported high levels of hybridization between *R. berlandieri* and *R. sphenoccephala* and attempted to show an intergradation from one species to the other through the zone of sympatry. However, all of their study sites (except one) within the sympatric zone of these two species were “man-made ponds.” At the one exception (their site #6) hybridization was markedly lower. It also should be noted that the two areas singled out by Lynch (1978) as having higher than average percentages of hybridization are both highly disturbed areas—one a recreation area and the other a fish hatchery.

Habitat isolation.—More important than temporal isolation in the sympatric zone of *R. pipiens* and *R. blairi* in Nebraska appears to be habitat isolation (Lynch, 1978). This isolating mechanism has also been reported as effective in segregating sympatric pairs of leopard frogs by Mecham (1968) in Arizona, and by Frost and Bagnara (1977b) in Mexico. Differing habitat associations were also noted in the present study. *R. berlandieri* is basically a stream breeder in central Texas—almost all of the natural habitat of this species in this area is along streams and rivers. It now breeds in artificial ponds and tanks as well as along streams, but in most areas where both types of habitat are available, *R. berlandieri* breeds more readily in pools along flowing water. On the contrary, I have never found *R. sphenoccephala* breeding in streams in

central Texas; I found this species breeding only in standing water (both temporary and permanent) in areas where it is sympatric with *R. berlandieri*. *R. blairi* typically breeds in flooded prairie pools and ponds in Texas, but breeds in some streams as well.

In southern Oklahoma, in the sympatric zone of *R. blairi* and *R. sphenoccephala*, both species were found breeding in stationary water as well as in streams. However, *R. blairi* was found more often in warmer, more turbid pools, and *R. sphenoccephala* in cooler, clearer streams and pools. In some areas habitat separation was obvious: in Sultan Park, Cotton County, 96% (n = 25) of the leopard frogs observed along East Cashe Creek (water temperature = 26 C on 12 July 1978) were *R. sphenoccephala*, whereas 87% (n = 15) of the leopard frogs observed in a shallow pond (water temperature = 39 C at the same time of same day) 100 m from East Cashe Creek were *R. blairi*. However, in several areas in nearby counties where habitats were less diverse, these two species were found virtually unseparated.

Ethological isolation.—Ethological isolation is undoubtedly important among leopard frogs, but few close observations of courtship behavior have been reported in the *R. pipiens* complex. The calls of leopard frogs have long been known to be different for various species (Bragg, 1950c; Littlejohn and Oldham, 1968; Mecham, 1971), and some studies indicate a differential attraction of females to conspecific males (Oldham, 1974). Another type of ethological isolation may involve differences in the call sites of males of different species. Frost and Bagnara (1977b) noted such a difference between males of *R. magnaocularis* and *R. forreri*. Tentative data gathered in this study suggest call site differences between males of *R. berlandieri*, *R. blairi* and *R. sphenoccephala*. *R. berlandieri* usually call from at or very close to shore, *R. blairi* often call from a floating position on the surface of the water, and *R. sphenoccephala* usually call mostly to completely submerged. In addition, *R. sphenoccephala* is the only species of leopard frog in central Texas which I have observed to oviposit during daylight hours.

Postmating isolation.—Studies of postmating isolating mechanisms in the *R. pipiens* complex (Moore, 1946a, 1946b, 1947, 1950, 1955, 1966, 1967a, 1967b; Mecham, 1969; Frost and Bagnara, 1976, 1977b) generally have demonstrat-

ed only slightly reduced fertility among sympatric species (the lowest fertility reported for a combination of the Texas species was a cross between a female *R. berlandieri* and a male *R. blairi* reported by Mecham, 1969, in which 73.5% of the cleaving eggs developed into larvae). However, most of the studies involving sympatric species of leopard frogs have not come from sympatric localities. The studies of Frost and Bagnara (1976, 1977b) are a notable exception; they did cross frogs from sympatric localities in Mexico and noted an unusual unidirectional success in artificial hybridization experiments. Specimens of the Texas leopard frogs from sympatric localities have yet to be artificially crossed. Some kind of postmating isolating mechanisms (probably a combination of hybrid inferiority and reduced hybrid fertility) presumably must cause selection against interspecific matings, which results in the reinforcement of reproductive character displacement evident in the reduced breeding seasons of sympatric compared to allopatric populations of leopard frogs in Texas.

SUMMARY AND CONCLUSIONS

Premating isolating mechanisms among sympatric combinations of *R. berlandieri*, *R. blairi* and *R. sphenoccephala* are well developed. Temporal isolation is apparently the most important; the breeding seasons of these three species are more differentiated in sympatry than in allopatry, presumably due to reinforcement of displacement through selection against interspecific matings. Habitat differentiation shows sympatric displacement to a much lesser degree, probably due to adaptation in allopatry before the ranges of these leopard frogs met. Sympatric displacement has also not been shown to occur in several ethological differences (including mating call and calling site differentiation). It is probable that hybrids are more poorly adapted to either parental habitat than are nonhybrids, so that habitat differentiation is one reason for hybrid inferiority. This postmating selection against interspecific matings has likely been the mechanism by which displacement of the breeding seasons has taken place.

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DEPARTMENT OF BIOLOGY, BAYLOR UNIVERSITY, WACO, TEXAS 76798. Accepted 26 May 1980.

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Systematics of the *Menidia beryllina* Complex (Pisces: Atherinidae) from the Gulf of Mexico and its Tributaries

BARRY CHERNOFF, JOHN V. CONNER AND CHARLES F. BRYAN

The *Menidia beryllina* complex from the Gulf of Mexico and Gulf slope drainages includes those forms referred to *M. audens*, *M. beryllina*, *M. beryllina atrimentis*, *M. beryllina peninsulae*, *M. peninsulae* and *M. peninsulae atrimentis*. The relationship between the Mississippi Valley form (*M. audens*) and the coastal form (*M. beryllina*) is clinal for several purportedly diagnostic characters, and within populations, character variation is often large and differences between size classes are noted. Variation of the *M. beryllina* phenotype is also found in other rivers. The relationship between *M. beryllina* and *M. peninsulae* has been obscured by historical treatment. *Menidia peninsulae*, from Florida to Tamaulapa, Mexico, can be distinguished by several morphometric and vertebral characteristics. We conclude that *M. audens*, *M. beryllina atrimentis* and *M. peninsulae atrimentis* are synonyms of *M. beryllina* and that *M. peninsulae* is a distinct species; a redescription of *M. peninsulae* is included.

FISHES of the genus *Menidia* Bonaparte currently comprise six recognized species (*M. audens* Hay, *M. beryllina* (Cope), *M. colei* Hubbs, *M. conchorum* Hildebrand and Ginsburg, *M. extensa* Hubbs and Raney, *M. menidia* (Linnaeus) and one questionable form (*M. peninsulae* (Goode and Bean)). These silversides inhabit coastal waters, rivers, streams and lakes from Nova Scotia to the Yucatan Peninsula.

The *M. beryllina* complex includes those forms which have been variously referred to as *M. audens*, *M. beryllina*, *M. beryllina atrimentis*, *M.*

beryllina cerea, *M. beryllina peninsulae*, *M. peninsulae* and *M. peninsulae atrimentis*. *Menidia beryllina cerea* Kendall, 1902, which is peripheral to this study (distributed from Massachusetts to South Carolina), has long been considered a synonym of *M. beryllina* (Jordan and Hubbs, 1919; Robbins, 1969). The other taxa, although common, have proved enigmatic and controversial with respect to delimitable species or subspecies (Kendall, 1902; Carr, 1936; Gosline, 1949; Robbins, 1969; Johnson, 1975; Edwards et al., 1978). This study is an attempt to clarify