

GENETIC VARIATION AND SYSTEMATIC DIVERSITY IN THE  
GHOST SHRIMP GENUS *LEPIDOPHTHALMUS* (DECAPODA:  
THALASSINIDEA: CALLIANASSIDAE)

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A B S T R A C T

The resurrected genus *Lepidophthalmus* defines a group of estuarine burrowing shrimp, western Atlantic members of which were until recently treated as a single homogeneous species. Individuals from fourteen Gulf of Mexico, two Caribbean, and one eastern Pacific localities were assayed by allozyme electrophoresis of 19 presumptive loci. Results were evaluated by principal components analysis of individual polymorphic allele data for definition of populations. Allozyme data were used to compare populations by *F*-statistics and measurement of pairwise genetic distances. Populations of *Lepidophthalmus* from within the Gulf of Mexico resolve into three distinct genetic lineages, pairwise genetic distances of which are comparable to congeneric species-level taxa in other invertebrate groups. The most widespread lineage defines *L. louisianensis* and consists of all samples from the northern through northwestern Gulf. This species is both geographically and allozymically separated from two other lineages (*Lepidophthalmus* sp. "a" and *Lepidophthalmus* sp. "b") that occurred sympatrically in a restricted area of the southwestern Gulf of Mexico, providing the first account of sympatric distribution in the genus. Taxonomic status for the southwestern Gulf lineages remains unresolved, but both are allozymically distinct from the Caribbean congeners, *L. jamaicense* and *L. sinuensis*, as well as the eastern Pacific species, *L. nr. bocourti*.

Revisions within the ghost shrimp family Callianassidae have partitioned the western Atlantic species that were formerly treated under *Callianassa* into a number of new and resurrected genera (Manning and Felder, 1991, 1992; Manning and Lemaitre, 1994), resulting in morphologically-based groupings of congeneric species that are generally similar in functional biology and habitat. Of the American genera, one of the more uniquely specialized is *Lepidophthalmus*, Holmes 1904, a taxon comprised largely (if not exclusively) of species that are adapted to organically enriched sediments of oligohaline environments and that have abbreviated larval life histories (Felder, 1978; Felder *et al.*, 1986; Lemaitre and Rodrigues, 1991; Manning and Felder, 1991; Felder and Rodrigues, 1993; Felder and Manning, 1997, 1998; Nates *et al.*, 1997; Nates and Felder, 1998, 1999). Such characteristics suggest a high potential for isolation of populations in this genus and thus a high potential for endemism.

Beyond generic revisions, studies on American callianassids have also addressed lower

taxonomic levels, particularly cases of taxonomic confusion or where wide-ranging species appeared to vary in morphology or functional biology. Such is the case with western Atlantic ghost shrimp now assigned to *Lepidophthalmus*, especially those of the Gulf of Mexico that have been assigned at various times to *Callianassa jamaicense* var. *louisianensis* Schmitt, 1935, *C. jamaicense* Schmitt, 1935 (sometimes with the alternative spelling *jamaicensis*), or *C. louisianensis* (Schmitt, 1935). The complete history of this taxonomic confusion was reviewed by Felder and Rodrigues (1993), who furnished a morphological redescription of *L. louisianensis* (Schmitt, 1935) from the northern Gulf of Mexico and defended its recognition at the species level. They identified a number of morphological characters to distinguish this species from a closely related congener in Brazil, with which it formerly had been confused, and provided characters to distinguish both the Gulf and Brazilian populations from those in Jamaica and others in the eastern Pacific. In addition, they noted abrupt regional

Table 1. Collection localities (abbreviated form in parentheses), geographical coordinates, numbers of individuals collected (*n*), and dates of collection for samples of *Lepidophthalmus* spp.

Locality	Coordinates	<i>n</i>	Date
<i>Lepidophthalmus louisianensis</i> :			
1. bayshore, Choctawhatchee Bay, Florida (CBFL)	30°26'N, 86°36'W	31	26 Apr 90
2. bayshore, Gulf Shores, Alabama (GSAL)	30°18'N, 87°45'W	30	09 Aug 90
3. bayshore, Dauphin Island, Alabama (DIAL)	30°16'N, 88°11'W	30	12 Nov 89
4. upper site, Bay St. Louis, Mississippi (UBMS)	30°20'N, 89°21'W	30	03 Oct 89
5. lower site, Bay St. Louis, Mississippi (LBMS)	30°21'N, 89°21'W	30	03 Oct 89
6. tidal pond, Grande Terre, Louisiana (GTLA)	29°17'N, 89°56'W	18	25 May 88
7. tidal pond, Grand Isle, Louisiana (GILA)	29°15'N, 90°01'W	20	16 Dec 87
8. tidal pond, Grand Isle, Louisiana (G2LA)	29°15'N, 90°01'W	25	20 Jan 89
9. Holly Beach, Louisiana (HBLA)	29°47'N, 93°28'W	30	20 Dec 87
10. Bayside, Texas (BSTX)	28°12'N, 97°01'W	27	03 Aug 90
11. Rio Grande River, Texas (RGTX)	25°58'N, 97°10'W	30	26 Jun 91
12. La Pesca, Tamaulipas, Mexico (LPTM)	23°47'N, 97°48'W	22	31 Mar 91
13. Barra del Tordo, Tamaulipas, Mexico (BTM)	22°42'N, 97°51'W	12	31 Mar 91
Indeterminate <i>Lepidophthalmus</i> spp.:			
14. Anton Lizardo, Veracruz, Mexico (ALVM)	18°58'N, 95°58'W	35	29 Mar 91
15. Puerto Ceiba, Tabasco, Mexico (PCTM)	18°23'N, 93°25'W	37	28 Mar 91
16. Nuevo Campechito, Campeche, Mexico (NCCM)	18°26'N, 92°07'W	33	27 Mar 91
Species from outside Gulf of Mexico:			
17. <i>L. sinuensis</i> , Rio Sinú estuary, Colombia (LSCO)	08°55'N, 76°27'W	42	16 Sep 90
18. <i>L. nr. bocourti</i> , Panama (LBPA)	08°59'N, 79°28'W	36	10 Sep 90
19. <i>L. jamaicense</i> , Mosquito Cove, Jamaica (MCJA)	18°33'N, 77°53'W	30	30 Nov 91

transitions in morphology of the southwestern Gulf populations that suggested presence of additional taxa along tropical coasts of the Gulf of Mexico. Most strikingly, variation was noted in the armature on ventral surfaces of the abdominal somites, with some individuals from southwestern Gulf exhibiting strong patterns of sclerotized ventral tubercles and plates, much as those reported or figured for *L. jamaicense*, *L. richardi* Felder and Manning, 1997, *L. sinuensis* Lemaitre and Rodrigues, 1991, and eastern Pacific members of the *L. bocourti* (A. Milne Edwards, 1870)/*L. eiseni* Holmes, 1904, complex (Felder and Manning, 1997, 1998; Felder and Staton, 2000).

The present paper reports allozymic analyses of the *Lepidophthalmus* complex from throughout the Gulf of Mexico, as well as for a sample of the topotypic population of *L. jamaicense* from Jamaica, a sample of *L. sinuensis* from the Caribbean coast of Colombia, and a sample from the *L. bocourti* complex taken on the Pacific coast of Panama, hereafter referred to as *L. nr.* (= near) *bocourti*. The latter taxa were included for comparison of taxonomically indeterminate Gulf of Mexico lineages to congeners that varied in both degree of morphological difference and distance of geographic separation.

## MATERIALS AND METHODS

Animals used for genetic analyses were collected (16 Dec 1987 to 30 Nov 1991) from single localities in coastal Colombia, Panama, and Jamaica, as well as from sites at intervals along shorelines of the Gulf of Mexico, particularly to either side of geographical features that could potentially account for breaks in distribution (Table 1, Fig. 1). All specimens of *Lepidophthalmus* were taken from low-salinity (0–20 ppt) intertidal flats and shorelines of muddy sand and sandy mud by extracting animals with a hand-operated, suction-coring device known as a yabby pump (see Hailstone and Stephenson, 1961; Manning, 1975) or by flushing animals from deep within the sediments they inhabit with a gasoline-driven water pump (Felder, 1978). If more than 30 individuals were obtained per site, representative intact specimens, in addition to remnants of individuals after tissue extraction, were preserved as morphological vouchers and archived in zoological collections of the University of Louisiana–Lafayette (ULLZ), the National Museum of Natural History, Smithsonian Institution, Washington (USNM), and the Colección Nacional de Crustáceos, Instituto de Biología (CNCR-IB) of the Universidad Nacional Autónoma de México (UNAM) (as cataloged by Felder and Staton, in press). In one locality, duplicate samples were taken from the exact same location (GILA and G2LA) on different dates, while in another case, samples were taken on the same date from sites within 100 m of each other (UBMS and LBMS).

Tissue samples were frozen in liquid nitrogen in the field or dissected from animals transported live to the laboratory and then stored at –70°C until analyzed. Techniques for allozyme analysis by starch gel electrophoresis followed Felder and Staton (1994). An initial screening of more than 35 enzymes produced 19 presumptive loci that were resolvable consistently. Allelic forms of en-

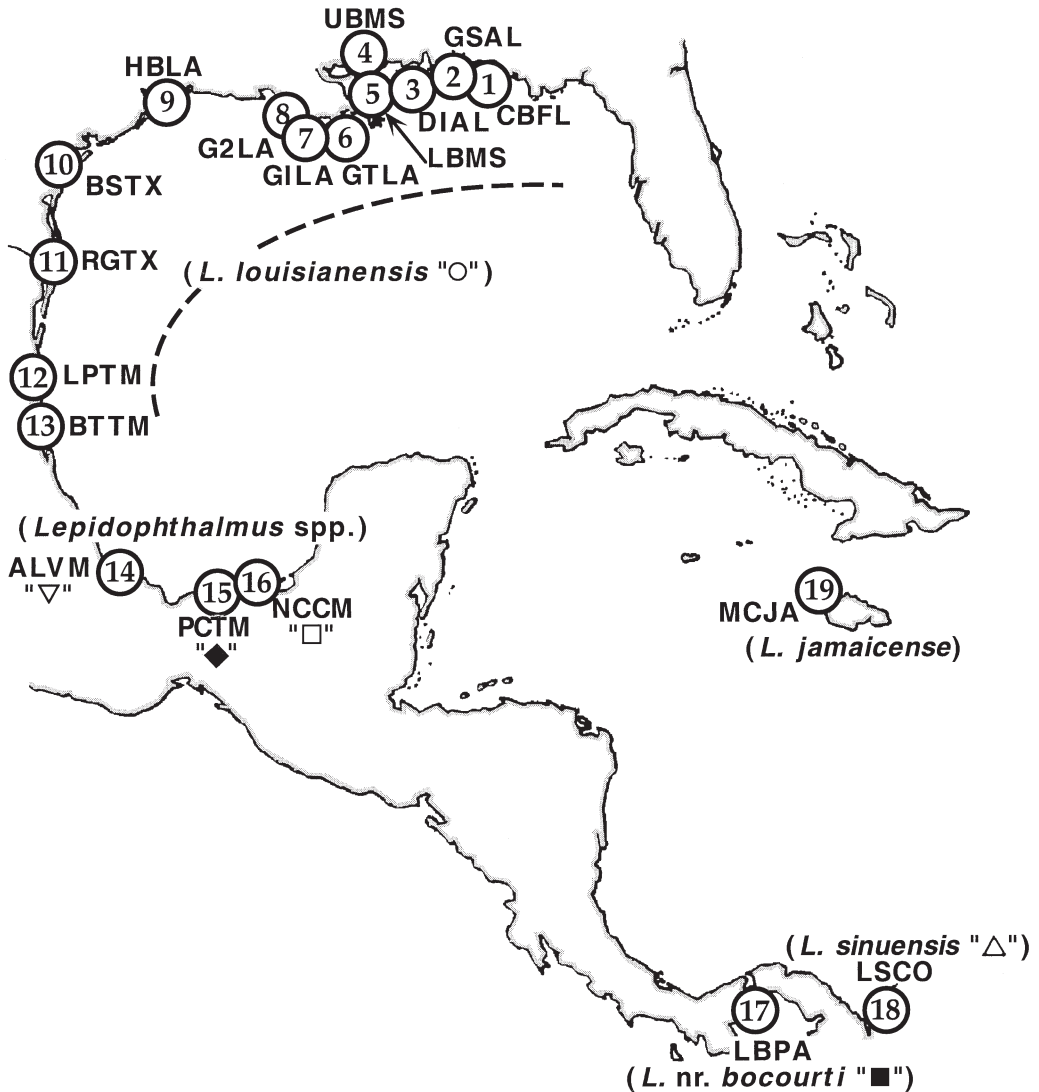


Fig. 1. Sample localities (Table 1) for putative *L. louisianensis* from the northwestern Gulf of Mexico, indeterminate populations of *Lepidophthalmus* spp. from the southwestern Gulf of Mexico, and congeners from outside the Gulf of Mexico. Symbols shown in quotation marks adjacent to each taxonomic group correspond to principal component scores in Fig. 2.

zymes (Tables 2 and 3) were designated alphabetically, "A" being the fastest migrating allele; different loci for the same enzyme system were designated by Arabic numeral. In the following list, loci marked with an asterisk (\*) were homozygous across the entire complex: Alanopine dehydrogenase\* (*Aladh*); Arginine kinase (*Ark*); Aspartate aminotransferase (*Aat*) 1 & 2, also called glutamic-oxaloacetic transaminase; Hexokinase (*Hk*) 1\* & 2\*; L-iditol dehydrogenase (*Iddh*), also called sorbitol dehydrogenase; Indophenol oxidase\* (*Ipo*), also called superoxide dismutase; Isocitric dehydrogenase (*Idh*) 1 & 2; Lactic dehydrogenase\* (*Ldh*); Malic dehydrogenase (*Mdh*) 1 & 2; Mannose phosphate isomerase (*Mpi*); 6-phosphogluconic dehydrogenase (*Pgdh*); Phosphoglucomutase (*Pgi*), also called glucose phosphate iso-

merase; and Phosphoglucomutase (*Pgm*). Two loci not included in Felder and Staton (1994) were screened in this study, both resolved on a Tris-citrate pH 8.0 buffer system: Leucine aminopeptidase (*Lap*, Enzyme Commission Number 3.4.11.-), also called cytosolic aminopeptidase, which was demonstrated with L-Leucine  $\beta$ -naphthylamide as substrate and Esterase\* (*Est*, E. C. Number 3.1.-.-), demonstrated with 4-methylumbelliferyl acetate as substrate.

A principal components (PC) analysis, based upon presence or absence of variable alleles, was performed on individuals as described in Liu *et al.* (1991). Individuals lacking genotypic information at one or more of the loci were excluded from the analysis; this excluded the Jamaican sample of *L. jamaicense* (MCJA) for which geno-

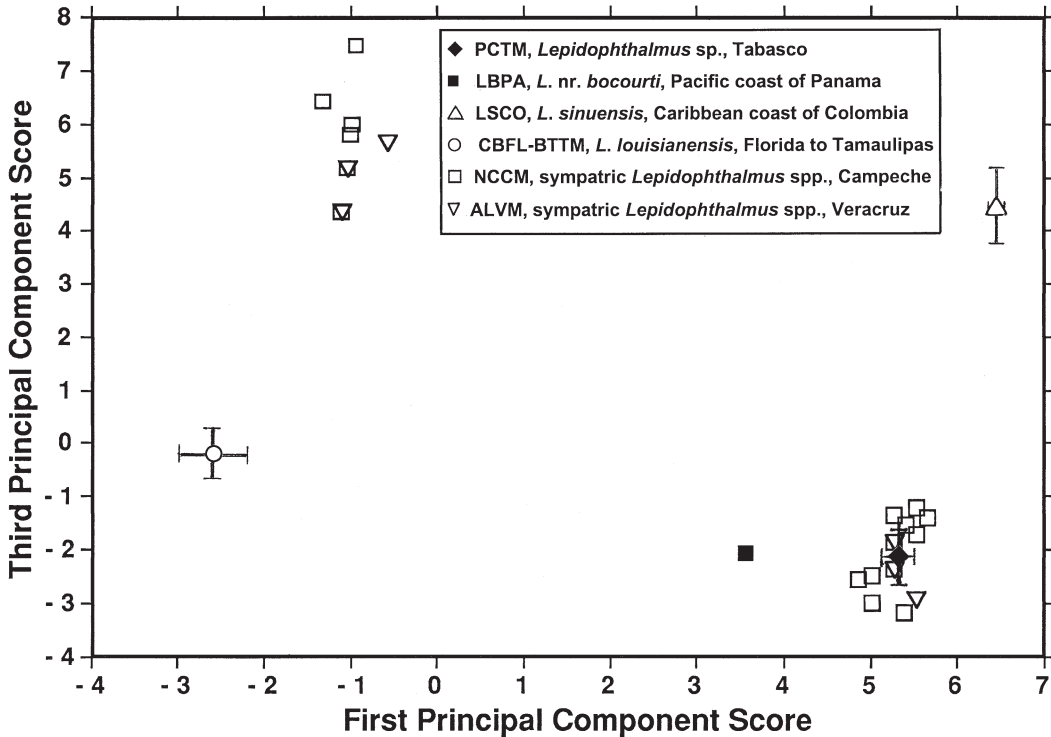


Fig. 2. First and third principal component scores based on polymorphic alleles for individuals comprising 18 samples of *Lepidophthalmus* spp. taken from localities in the western Atlantic and on the Pacific coast of Panama (Table 1, Fig. 1, excluding sample no. 19, MCJA). Data for those localities inhabited by a single species are shown as sample means  $\pm$  one standard deviation (vertical and horizontal bars; zero for LBPA where all individuals share same multi-locus genotype). Data for localities inhabited by sympatric species are shown for individual observations.

typic information was missing for the *Aat-1* locus and 19 additional individuals from other samples with missing data, giving a total sample size of 497 for the PC analysis. Allelic frequencies and observed heterozygosities ( $H_{OBS}$ ) for each locus were determined by direct census of population data, and expected heterozygosities ( $H_{EXP}$ ) within populations were determined as mean values across samples. The frequency of polymorphic loci by the 95% criterion ( $P_{95}$ , *sensu* Swofford and Selander, 1981), hierarchical  $F$ -statistics ( $F_{IS}$  and  $F_{ST}$ , Weir and Cockerham, 1984), and genetic distance ( $D_N$ , Nei, 1972) were also calculated as previously. Distances were clustered using both the unweighted pair-group algorithm (=UPGMA, Sneath and Sokal, 1973) and the neighbor-joining algorithm (Nei, 1991; Saitou and Nei, 1987).

## RESULTS

The first, second, and third principal component (PC) scores explained 24.9%, 13.4%, and 7.2%, respectively, of the total allelic variation among individuals. The fourth, fifth, and sixth PC scores each explained less than 4% of the total variance and were not considered further. The second PC axis primar-

ily separated the Pacific Panamanian sample of *L. nr. bocourti* (LBPA) from the other samples (details not shown). Because this sample was also differentiated from the others on the basis of first PC scores, we plotted the third PC score versus the first PC score for two-dimensional display of groupings among samples (Fig. 2). Given the limited genetic differentiation among northern and western Gulf samples from Florida to Tamaulipas, Mexico, all of which putatively represented *L. louisianensis* and shared common alleles (Table 2), we plotted mean PC scores and error bars across those thirteen samples, rather than individual PC scores. Samples from Tabasco, Mexico (PCTM) and Colombia (LSCO) also had limited inter-individual genetic differences and were likewise plotted as means for visual clarity. This bivariate scatterplot suggested the existence of five discrete clusters of individuals, one of which corresponded to *L. nr. bocourti* (LBPA) and an-

Table 2. Allele frequencies at 11 polymorphic loci\* for samples of putative *Lepidophthalmus louisianensis* from collection localities (Table 1, Fig. 1) in the northern and western Gulf of Mexico. Dash denotes 0.00 values. Values of observed ( $H_{OBS}$ ) and expected ( $H_{EXP}$ ) heterozygosities are averaged across all loci.

Locus	Allele	CBFL	GSAL	DIAL	UBMS	LBMS	GTLA	GILA	G2LA	HBLA	BSTX	RGTX	LPTM	BTTM
<i>Aat-1</i>	A	—	—	0.03	0.03	0.03	—	—	—	—	—	—	—	—
	B	0.03	0.02	0.03	0.15	0.23	—	—	—	—	—	—	0.28	0.42
	C	0.97	0.98	0.94	0.82	0.74	1.00	1.00	1.00	1.00	1.00	1.00	0.72	0.58
<i>Aat-2</i>	A	—	—	—	0.02	—	—	—	0.02	0.02	—	—	—	—
	B	1.00	0.97	0.98	0.98	1.00	0.94	1.00	0.98	0.96	1.00	1.00	1.00	1.00
	C	—	0.03	0.02	—	—	0.06	—	—	0.02	—	—	—	—
<i>Ark</i>	B	—	—	—	—	—	—	—	—	—	—	0.02	—	—
	D	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98	1.00	1.00
<i>Iddh</i>	B	—	—	—	—	—	—	—	0.43	—	—	—	—	—
	C	0.70	0.67	0.32	0.45	0.35	0.55	0.33	0.07	0.33	0.46	0.95	1.00	1.00
	D	—	—	—	—	—	—	—	—	—	0.04	—	—	—
	E	0.30	0.33	0.65	0.55	0.63	0.45	0.67	0.50	0.60	0.46	0.05	—	—
	F	—	—	0.03	—	0.02	—	—	—	0.02	0.04	—	—	—
	G	—	—	—	—	—	—	—	—	0.05	—	—	—	—
	H	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Idh-1</i>	A	0.03	0.10	—	0.03	—	—	—	—	—	0.02	—	—	—
	B	0.97	0.90	1.00	0.97	1.00	1.00	1.00	1.00	1.00	0.98	1.00	1.00	1.00
<i>Lap</i>	A	—	—	—	—	—	—	—	0.02	—	—	—	—	—
	B	0.79	0.42	0.42	0.34	0.55	0.44	0.20	0.38	0.05	0.15	0.14	0.07	0.75
	C	0.04	0.13	0.07	0.179	0.10	0.24	0.18	0.29	0.38	0.17	0.55	0.59	0.17
	D	—	—	—	—	—	—	—	—	—	0.04	—	—	—
	E	0.17	0.45	0.51	0.48	0.33	0.32	0.62	0.31	0.57	0.64	0.31	0.34	0.08
	F	—	—	—	—	0.02	—	—	—	—	—	—	—	—
<i>Mdh-1</i>	A	—	—	—	—	—	—	—	—	—	0.04	0.60	0.36	0.38
	B	1.00	0.97	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.96	0.40	0.64	0.62
	C	—	0.03	—	—	—	—	—	—	—	—	—	—	—
<i>Mdh-2</i>	A	—	0.07	—	—	—	—	—	—	—	0.07	—	0.02	—
	B	1.00	0.93	1.00	1.00	1.00	1.00	0.92	0.98	1.00	0.93	—	0.98	1.00
	C	—	—	—	—	—	—	0.08	0.02	—	—	—	—	—
	D	—	—	—	—	—	—	—	—	—	—	1.00	—	—
<i>Pgdh</i>	A	1.00	1.00	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	B	—	—	0.02	—	—	—	—	—	—	—	—	—	—
<i>Pgi</i>	A	—	—	—	0.02	—	—	—	—	—	—	0.07	—	—
	B	—	0.02	—	—	—	—	—	—	—	—	—	—	—
	C	0.05	0.52	0.66	0.72	0.72	0.61	0.75	0.76	0.52	0.41	0.17	0.25	0.21
	D	0.95	0.46	0.32	0.18	0.28	0.39	0.25	0.24	0.48	0.57	0.76	0.75	0.79
	G	—	—	0.02	0.08	—	—	—	—	—	0.02	—	—	—
<i>Pgm</i>	B	—	0.02	—	—	—	—	—	—	—	—	—	—	—
	D	—	—	—	—	—	0.14	—	0.08	0.02	—	—	—	—
	E	0.93	0.91	0.60	0.63	0.75	0.50	0.77	0.67	0.75	0.71	0.87	1.00	1.00
	G	—	0.02	0.20	0.15	0.10	0.36	0.10	0.08	0.16	0.09	0.08	—	—
	H	0.05	0.05	0.17	0.15	0.15	—	0.10	0.15	0.05	0.13	0.05	—	—
	I	0.02	—	0.03	0.07	—	—	0.03	0.02	0.02	0.07	—	—	—
	H <sub>OBS</sub> (SE)	0.04	0.09	0.10	0.10	0.11	0.12	0.08	0.09	0.10	0.09	0.09	0.09	0.11
H <sub>EXP</sub> (SE)	0.06	0.12	0.12	0.13	0.12	0.12	0.10	0.12	0.11	0.12	0.10	0.10	0.10	0.09
H <sub>OBS</sub> (SE)	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.04	0.03	0.02	0.03	0.03	0.03	0.04

\*The *Est*, *Hex-1*, *Hex-2*, *Ipo*, *Ldh*, and *Mpi* loci were monomorphic for allele B; the *Aladh* locus was monomorphic for allele B; the *Idh-2* locus was monomorphic for allele D.

other to *L. sinuensis* (LSCO). One of the remaining three clusters was composed of all aforementioned samples from Florida to Tamaulipas, Mexico, and corresponded to nominal *L. louisianensis*. Another cluster (denoted *Lepidophthalmus* sp. “b”) consisted of three individuals from Veracruz (ALVM) and 13 individuals from Campeche (NCCM). In some analyses below, two additional indi-

viduals from Veracruz and one additional individual from Campeche were also treated as members of this cluster because of overall similarity of the multi-locus genotype, even though they were excluded from the PC analysis due to missing genotypic information for *Aat-1* or *Pgm*.

The remaining cluster (*Lepidophthalmus* sp. “a”) consisted of all 37 individuals from

Table 3. Allele frequencies at 14 polymorphic loci\* for samples of *Lepidophthalmus* spp. from collection localities (Table 1, Fig. 1) in the southwestern Gulf of Mexico (*Lepidophthalmus* spp. "a" and "b"), the Caribbean coast of Colombia (*L. s.* = *L. sinuensis*), the Pacific coast of Panama (*L. nr. b.* = *L. nr. bocourti*), and Jamaica (*L. j.* = *L. jamaicense*). Dash denotes 0.00 values; "md" denotes missing data. Values of observed ( $H_{OBS}$ ) and expected ( $H_{EXP}$ ) heterozygosities are averaged across all loci.

Locus	Allele	<i>Lepidophthalmus</i> sp. "a"			<i>Lepidophthalmus</i> sp. "b"		<i>L. s.</i>	<i>L. nr. b.</i>	<i>L. j.</i>
		ALVM	PCTM	NCCM	ALVM	NCCM	LSCO	LBPA	MCJA
<i>Aat-1</i>	A	—	—	—	1.00	1.00	1.00	1.00	md
	D	1.00	1.00	1.00	—	—	—	—	md
<i>Aat-2</i>	A	1.00	1.00	1.00	—	—	1.00	—	—
	B	—	—	—	0.90	1.00	—	—	1.00
	C	—	—	—	0.10	—	—	1.00	—
<i>Aladh</i>	A	—	—	—	—	—	—	—	1.00
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—
<i>Ark</i>	A	—	—	—	—	—	—	1.00	—
	B	—	—	—	—	—	—	—	1.00
	C	—	0.05	0.13	1.00	1.00	1.00	—	—
	D	1.00	0.95	0.87	—	—	—	—	—
<i>Iddh</i>	A	—	0.05	—	—	—	—	1.00	—
	B	1.00	0.95	1.00	—	—	1.00	—	0.02
	C	—	—	—	1.00	0.96	—	—	0.98
	E	—	—	—	—	0.04	—	—	—
<i>Idh-1</i>	A	—	—	—	—	0.04	—	—	—
	B	0.98	1.00	1.00	1.00	0.96	1.00	1.00	0.95
	C	0.02	—	—	—	—	—	—	0.05
<i>Idh-2</i>	A	—	—	0.24	—	—	—	1.00	—
	B	1.00	1.00	0.76	—	—	1.00	—	—
	C	—	—	—	1.00	1.00	—	—	—
	D	—	—	—	—	—	—	—	1.00
<i>Ldh</i>	A	—	—	—	—	—	—	—	1.00
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—
<i>Lap</i>	B	—	—	—	—	—	—	—	0.18
	C	—	—	—	1.00	1.00	—	—	0.74
	E	—	—	—	—	—	—	—	0.08
	F	1.00	1.00	1.00	—	—	0.62	—	—
	G	—	—	—	—	—	0.38	—	—
	H	—	—	—	—	—	—	1.00	—
<i>Mdh-1</i>	A	—	—	—	—	—	—	—	1.00
	B	—	—	—	1.00	1.00	—	—	—
	C	0.60	0.81	0.76	—	—	—	—	—
	D	0.40	0.19	0.24	—	—	1.00	1.00	—
<i>Mdh-2</i>	A	—	—	—	—	—	—	—	0.02
	B	—	—	—	1.00	1.00	—	—	0.98
	D	1.00	1.00	1.00	—	—	1.00	1.00	—
<i>Pgdh</i>	A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—
	B	—	—	—	—	—	—	—	1.00
<i>Pgi</i>	A	—	—	—	—	—	1.00	—	—
	C	1.00	1.00	1.00	—	—	—	—	—
	D	—	—	—	0.60	0.18	—	1.00	0.98
	E	—	—	—	0.40	0.82	—	—	0.02
<i>Pgm</i>	A	—	—	0.03	—	—	—	—	—
	B	1.00	1.00	0.94	—	—	0.98	—	—
	C	—	—	—	—	—	—	—	0.02
	D	—	—	0.03	—	—	—	—	0.98
	E	—	—	—	—	—	—	1.00	—
	F	—	—	—	—	—	0.02	—	—
	G	—	—	—	1.00	0.96	—	—	—
J	—	—	—	—	0.04	—	—	—	
$H_{OBS}$		0.04	0.02	0.05	0.03	0.02	0.02	0.00	0.03
(SE)		0.01	0.01	0.01	0.02	0.01	0.01	0.00	0.01
$H_{EXP}$		0.03	0.03	0.06	0.04	0.03	0.03	0.00	0.04
(SE)		0.01	0.02	0.03	0.04	0.03	0.01	0.00	0.02

\* The *Est*, *Hex-1*, *Hex-2*, *Ipo*, and *Mpi* loci were monomorphic for the B allele.

Table 4. Hierarchical  $F$ -statistics for samples of *Lepidophthalmus* spp. from the Gulf of Mexico. Dash denotes monomorphic loci for which statistic could not be estimated.

Locus	<i>L. louisianensis</i>		<i>Lepidophthalmus</i> sp. "a"		<i>Lepidophthalmus</i> sp. "b"	
	$F_{ST}$	$F_{IS}$	$F_{ST}$	$F_{IS}$	$F_{ST}$	$F_{IS}$
<i>Aat-1</i>	0.16	0.42	—	—	—	—
<i>Aat-2</i>	0.00	-0.01	—	—	0.12	-0.06
<i>Ark</i>	0.00	0.00	0.05	0.16	—	—
<i>Iddh</i>	0.25	0.12	0.02	0.49	-0.05	0.02
<i>Idh-1</i>	0.04	0.14	0.00	0.00	-0.05	0.02
<i>Idh-2</i>	0.04	1.00	0.25	0.58	—	—
<i>Lap</i>	0.15	0.35	—	—	—	—
<i>Mdh-1</i>	0.42	-0.04	0.05	-0.24	—	—
<i>Mdh-2</i>	0.82	0.60	—	—	—	—
<i>Pgdh</i>	0.00	0.00	—	—	—	—
<i>Pgi</i>	0.22	0.00	—	—	0.28	0.28
<i>Pgm</i>	0.07	0.02	0.03	-0.02	-0.04	0.02
Jackknife Mean	0.24	0.16	0.05	-0.17	0.30	0.26
Standard Error	0.06	0.09	0.05	0.31	0.17	0.16

Tabasco (PCTM), 30 individuals from the aforementioned Veracruz locality (ALVM) and 18 individuals from Campeche (NCCM). As before, one additional individual from Campeche was also treated in subsequent analyses as a member of this cluster, even though it was excluded from the PC analysis because it lacked data for *Pgi*. For specimens from the Veracruz (ALVM) and Campeche (NCCM) localities that were separated into two non-overlapping clusters, sympatric individuals belonging respectively to *Lepidophthalmus* spp. "a" versus "b" differed genotypically in that they varied for anomalous allelic types at the *Aat-1*, *Aat-2*, *Iddh*, *Idh-2*, *Mdh-1*, *Mdh-2*, and *Pgi* loci (Table 3). No individuals in collections from either of these two sites (ALVM or NCCM) were heterozygous for alleles characteristic of the separate clusters, suggesting the absence of interbreeding individuals. At the time collections were made, morphological differences between these two groups of individuals were not apparent, although it did appear that there were two distinct size classes within the small areas sampled (< 0.25 hectare).

Mean number of alleles per locus ( $\pm$  SE) among *Lepidophthalmus* spp. ranged from  $1.00 \pm 0.00$  for the sample of *L. nr. bocourti* from Panama (fixed for the same allele at all 19 loci) to  $1.74 \pm 0.26$  for a sample of *L. louisianensis* from Texas (Tables 2, 3). Frequency of polymorphism at the 95% criterion within Gulf populations ranged from 0.0 in the Panamanian sample to 31.6 in a sample of *L. louisianensis* from Alabama. In general,

observed and expected heterozygosities were higher in *L. louisianensis* than in lineages separated as *Lepidophthalmus* spp. "a" and "b." However, it is unclear whether this is an effect within the lineage or an effect of geographic location, because the southernmost collection of *L. louisianensis* from Tamaulipas, Mexico, also showed low heterozygosity (Tables 2, 3). Most of the higher heterozygosity can be attributed to the higher number of alleles per locus for *L. louisianensis*, since the mean inbreeding coefficient across all loci (jackknife mean  $F_{IS}$ ) suggests a deficiency of heterozygotes within populations (Table 4). The  $F_{ST}$  values for *L. louisianensis* and *Lepidophthalmus* sp. "b" suggest genetic divergence among sampling sites, which is not the case for *Lepidophthalmus* sp. "a".

In general, common alleles in the northern through western Gulf samples of *L. louisianensis* (Table 2) became rare or undetectable in the southwestern Gulf, except for some loci in which alleles were shared with samples of the southwestern Gulf lineage termed *Lepidophthalmus* sp. "b" (Table 3). *Pgm*<sup>e</sup> was the common allele in the polymorphic northern through northwestern Gulf populations of *L. louisianensis* (CBFL to RGTX), became fixed in the western Gulf populations of this species (LPTM and BTTM), and was replaced by two alternative alleles in the southwestern Gulf. Allele frequencies of the *Aat* and *Gpi* loci supported this pattern. However, the *Aat-2* locus exemplified a pattern in which northern through western Gulf samples of *L. louisianensis* (CBFL to BTTM) grouped with sam-

Table 5. Matrix of genetic distances ordered by collection localities (Table 1, Fig. 1) for samples of *Lepidophthalmus* spp.; lower-left values for Nei's standard distance ( $D_N$ ); upper-right values for corresponding approximate standard errors, calculated according to formula 9.44 of Nei (1987). Symbols "a" and "b" represent southwestern Gulf of Mexico sympatric populations of *Lepidophthalmus* spp. "a" and "b", respectively.

MCJA	CBFL	GSAL	DIAL	UBMS	LBMS	GTLA	GILA	G2LA	HBLA	BSTX	RGTX	LPTM	BTTM	ALVM "a"	PCTM "a"	NCCM "a"	ALVM "b"	NCCM "b"	LSCO	LBPA
CBFL	—	0.04	0.05	0.05	0.05	0.05	0.06	0.06	0.05	0.04	0.08	0.05	0.03	0.20	0.20	0.20	0.11	0.12	0.23	0.18
0.21																				
GSAL	0.02	—	0.03	0.03	0.03	0.03	0.03	0.04	0.03	0.02	0.08	0.04	0.04	0.18	0.18	0.18	0.11	0.11	0.22	0.19
0.22																				
DIAL	0.05	0.02	—	0.01	0.01	0.02	0.02	0.03	0.02	0.02	0.09	0.06	0.06	0.18	0.18	0.18	0.11	0.11	0.22	0.20
0.22																				
UBMS	0.05	0.01	0.00	—	0.02	0.02	0.02	0.03	0.02	0.03	0.09	0.06	0.06	0.18	0.18	0.17	0.11	0.11	0.22	0.20
0.22																				
LBMS	0.04	0.01	0.00	0.00	—	0.02	0.02	0.03	0.03	0.03	0.09	0.06	0.06	0.18	0.18	0.18	0.11	0.12	0.22	0.20
0.23																				
GTLA	0.04	0.01	0.01	0.01	0.01	—	0.03	0.03	0.03	0.03	0.09	0.05	0.05	0.18	0.18	0.18	0.09	0.10	0.22	0.20
0.21																				
GILA	0.06	0.02	0.00	0.00	0.01	0.02	—	0.03	0.02	0.02	0.09	0.06	0.07	0.18	0.18	0.18	0.11	0.12	0.22	0.20
0.23																				
G2LA	0.06	0.03	0.01	0.01	0.01	0.02	0.01	—	0.03	0.04	0.10	0.07	0.07	0.16	0.17	0.16	0.11	0.12	0.21	0.20
0.23																				
HBLA	0.05	0.02	0.01	0.01	0.02	0.01	0.01	0.02	—	0.02	0.09	0.05	0.06	0.18	0.18	0.18	0.10	0.11	0.22	0.19
0.22																				
BSTX	0.03	0.01	0.01	0.01	0.02	0.02	0.01	0.03	0.01	—	0.08	0.05	0.05	0.18	0.18	0.18	0.10	0.11	0.22	0.19
0.21																				
RGTX	0.12	0.11	0.15	0.14	0.15	0.13	0.14	0.16	0.12	0.11	—	0.06	0.07	0.17	0.17	0.17	0.12	0.13	0.19	0.16

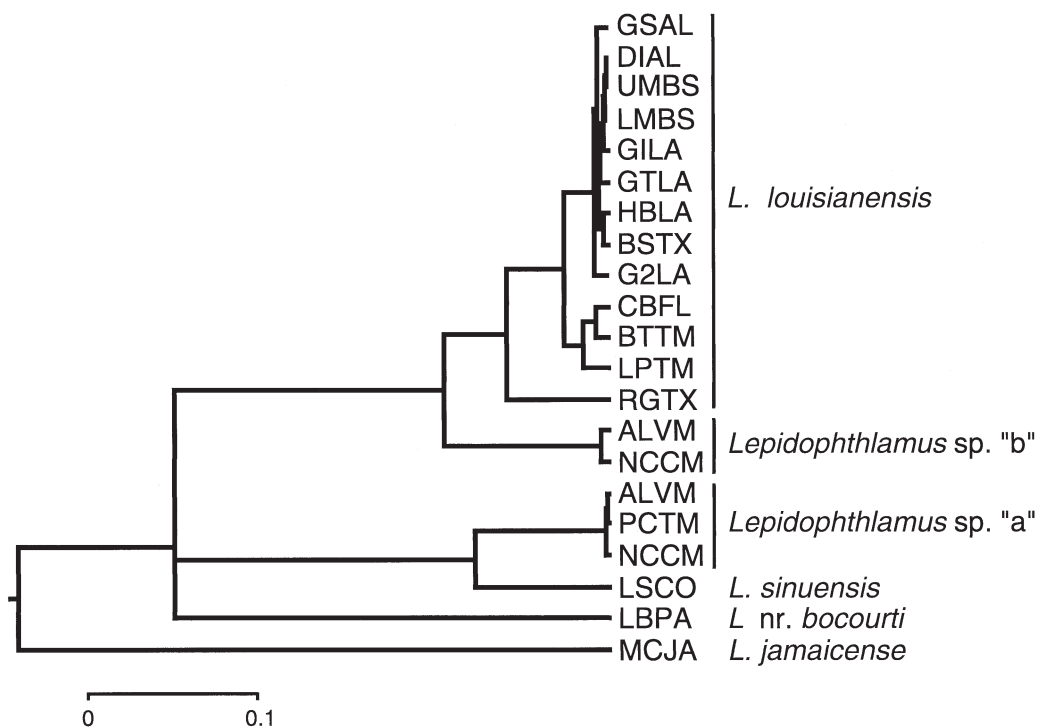


Fig. 3. Dendrogram derived by UPGMA cluster analysis for samples of *Lepidophthalmus* spp. by collection locality (Table 1, Fig. 1), based on Nei's standard distance ( $D_N$ ) derived from 18 presumptive loci; the 19th locus, *Aat-1*, was excluded from this analysis as these data were not available for specimens from the MCJA collection. Where applicable, sympatric lineages are separated and denoted as *Lepidophthalmus* spp. "a" and "b", respectively.

ples of *Lepidophthalmus* sp. "b" (ALVM and NCCM) by virtue of the shared *Aat-2<sup>c</sup>* allele, in contrast to southwestern Gulf samples of *Lepidophthalmus* sp. "a" (ALVM, PCTM, NCCM) in which this allele was replaced by *Aat-2<sup>b</sup>*. A near-identical grouping of populations occurred on the basis of several other allelic pairs, including *Iddh<sup>c</sup>* vs. *Iddh<sup>b</sup>*, *Idh-2<sup>d</sup>* vs. *Idh-2<sup>c</sup>*, *Mdh-1<sup>b</sup>* vs. both *Mdh-1<sup>c</sup>* and *Mdh-1<sup>d</sup>*, *Mdh-2<sup>b</sup>* vs. *Mdh-2<sup>d</sup>*, and to a lesser degree *Pep-2<sup>a</sup>* vs. *Pep-2<sup>c</sup>*.

When genetic distances (Table 5) are subjected to UPGMA analysis (Fig. 3), *L. jamaicense* is positioned at the base of a trichotomy separating groups constituted by *L. nr. bocourti*, *L. sinuensis* plus *Lepidophthalmus* sp. "a", and *L. louisianensis* plus *Lepidophthalmus* sp. "b". When genetic distances are clustered by a neighbor-joining tree rooted on *L. jamaicense*, *L. louisianensis* plus *Lepidophthalmus* sp. "b" group basally to a divergent clade composed of *L. nr. bocourti* and the closely associated *L. sinuensis* and *Lepidophthalmus* sp. "a" (Fig. 4). With the ex-

ception of a collection from the extreme south Texas locality (RGTX), there is little genetic distance among samples of the cosmopolitan species *L. louisianensis* and thus general consistency with the PC results.

#### DISCUSSION

An  $F_{ST}$  of approximately 0.2, as observed in *L. louisianensis* (Table 4), is similar to that noted for other sessile marine invertebrates (Kwast *et al.*, 1990). In general, the mean number of alleles per locus was higher within the *Lepidophthalmus* spp. complex than for confamilial members of the genus *Callichirus* (Staton and Felder, 1995). *Lepidophthalmus louisianensis* is known to have an abbreviated larval period of approximately three days with only two free-swimming, estuarine-adapted zoeal stages prior to metamorphosis into a burrowing postlarva (Felder *et al.*, 1986); recent studies suggest that abbreviated development (0–2 zoeal stages) and estuarine retention are characteristic of the genus *Lepidophthalmus* overall (Nates *et al.*, 1997), in

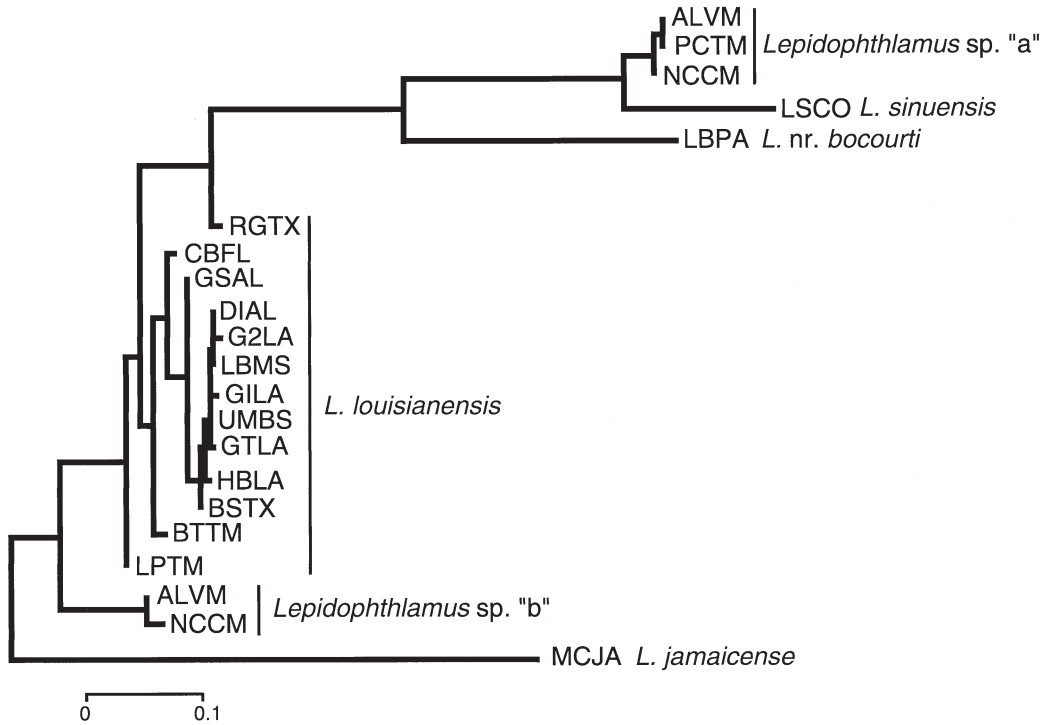


Fig. 4. Dendrogram derived by neighbor-joining method of analysis for samples of *Lepidophthalmus* spp. by collection locality (Table 1, Fig. 1), based on Nei's standard distance ( $D_N$ ) derived from 18 presumptive loci; the 19th locus, *Aat-1*, was excluded from this analysis as these data were not available for specimens from the MCJA collection. Where applicable, sympatric lineages are separated and denoted as *Lepidophthalmus* spp. "a" and "b", respectively.

contrast to some confamilials (Strasser and Felder, 1998, 1999). Estuarine crustaceans with abbreviated development tend to be retained within the parental estuary (Strathmann, 1982). This greatly limits dispersal between widely separated estuaries, favoring low heterozygosity and other effects on genetic structure (Fuller and Lester, 1980; Chow and Fujio, 1987). While no data exist for local extinction rates within *Lepidophthalmus* populations, long-term sampling of both the Grand Terre, Louisiana (GTLA), and lower Bay St. Louis, Mississippi (LBMS), sites has revealed large fluctuations in total population size and rates of recolonization (Felder and Griffis, 1994; D. L. Felder, unpublished). At least one dramatic population decline followed dense infestation of the burrows by predatory pink wormfish (Felder and Rodrigues, 1993).

Within *L. louisianensis*, all populations sampled from the northern through western Gulf region were genetically similar to one

another, with the RGTX sample being a slight exception. Considered as a group, the overall sample of *L. louisianensis* from the northern through western Gulf was markedly different from the Jamaican population (*L. jamaicensis*), the Colombian population (*L. sinuensis*), and the Panamanian Pacific population (*L. nr. bocourti*). It was also distinct from populations comprising two southwestern Gulf lineages, *Lepidophthalmus* spp. "a" and "b". These genetic observations, plus a comparison of these findings to those based upon morphology by Felder and Rodrigues (1993), support continued recognition of the northern through western Gulf population as the discrete taxon, *L. louisianensis*.

It is noteworthy that the easternmost sample of *L. louisianensis* from Florida (CBFL) showed greatest genetic similarity to samples from the Rio Grande River, Texas, and Tamaulipas, Mexico (RGTX to BTTM), in the extreme western Gulf. While unexpected, this pattern has also been reported previously

in population genetic studies of the thaidid gastropods (*Stramonita*) by Liu *et al.* (1991). Contemporary gene flow is improbable between these populations of *Lepidophthalmus*, given their wide geographic separation and the patterns of prevailing longshore currents between these geographic extremes, but there may also be some historical basis for this observation. In the *Menippe adina* Williams and Felder/*M. mercenaria* (Say) complex, the largely tropical stock of *M. mercenaria* replaces the northern Gulf endemic *M. adina* at both the northeastern-Gulf and southeastern-Gulf extremes of its range. In at least the northeastern-Gulf contact zone, there is introgressive hybridization between these sibling species (Bert, 1986; Williams and Felder, 1986; Bert and Harrison, 1988). A similar pattern, without documented hybridization, occurs in the Gulf endemic *U. spinicarpa* Rathbun, which is replaced by its tropical sibling *U. speciosa* (Ives) in both the northeastern Gulf and the southeastern Gulf (Barnwell and Thurman, 1983). The warm-temperate species of *Lepidophthalmus* may also be tropical in origin, especially since the closest congeners appear to be distributed antitropically, suggesting shared tropical origins (Felder and Rodrigues, 1993; Felder and Manning, 1997, 1998). Genetic similarity of eastern and western Gulf of Mexico population extremes is perhaps a relict of historical contact and introgression with common genetic stock, possibly predating postglacial expansion or re-expansion of coastal range into the northern Gulf of Mexico by way of separate eastern and western Gulf tracks. Extinction and recolonization rates in these animals argue against drift toward similar alleles at such range extremes by chance alone.

The PC and distance analyses revealed a large genetic discontinuity located between Barra del Tordo, Tamaulipas (BTTM), and Anton Lizardo, Veracruz (ALVM). This marks a southern transition in the western Gulf where *L. louisianensis* is replaced by two undescribed sympatric lineages (*Lepidophthalmus* spp. "a" and "b"), apparently endemic to the states of Veracruz, Tabasco, and Campeche, Mexico. Current morphologically based records establish a southern extreme of range for *L. louisianensis* to at least Tamiahua, in northern Veracruz (Felder and Rodrigues, 1993). This is in the general region (vicinity of Cabo Rojo) of other long-

noted warm-temperate to tropical transitions for varied coastal biotic assemblages (see Briggs, 1974; Britton and Morton, 1989).

There is no evidence of introgression between the two southwestern Gulf sympatric lineages herein represented as *Lepidophthalmus* spp. "a" and "b". They are separated at a genetic distance ( $D_N = 0.65$ ) comparable to or in excess of that which separates other species of the genus in our analyses. Although comparative morphological analysis and description of *Lepidophthalmus* sp. "b" are not completed, samples of *Lepidophthalmus* sp. "a" from the states of Veracruz (ALVM), Tabasco (PCTM), and Campeche (NCCM) are being assigned to a new species (Felder and Staton, 2000). Whereas individuals of *Lepidophthalmus* sp. "b" bear minimal armor on ventral surfaces of the abdomen, these surfaces are densely covered by sclerites in *Lepidophthalmus* sp. "a", a feature shared to varied degrees with *L. jamaicensis*, *L. richardi*, *L. sinuensis*, *L. nr. bocourti*, *L. bocourti*, *L. eiseni*, and at least one additional undescribed species from the eastern Pacific (Felder and Rodrigues, 1993; Felder and Manning, 1997, 1998).

Samples of *Lepidophthalmus* sp. "b" from Veracruz (ALVM) and Campeche (NCCM) are allozymically differentiated from samples of *L. louisianensis* at a  $D_N$  of 0.195, and resemble this species morphologically in their lack of ventral tuberculation. However, *Lepidophthalmus* sp. "b" also shares a unique characteristic with the overall more distant *L. sinuensis* from Colombia in that all samples of these two lineages are fixed for  $Ark^c$ . This could represent the vestige of a common Caribbean stock for these two groups, perhaps the source of immigrants to the southwestern Gulf by way of the Yucatán Straits. Even though *L. sinuensis* was recently found to have ventral sclerotization on the abdomen, it represents a group with atypically weak development of this character (Felder and Manning, 1997). However, our allozymic characterizations have not to date included *L. siri-boia* Felder and Rodrigues, another potential close relative in the western Atlantic that lacks ventral sclerotization and is an apparent southern antitropical counterpart to *L. louisianensis* inhabiting the coast of Brazil (Felder and Rodrigues, 1993). Precedent for recruitment and isolation of widely distributed Caribbean stocks in the southwestern

Gulf is seen in occurrences of other taxa, such as the singular record of the species *U. major* (Herbst) in Tabasco (Barnwell and Thurman, 1983).

Our analyses clearly separate the Jamaican population of *L. jamaicense* from other species of the genus and thereby contribute to resolving its long-confused relationship to populations in the Gulf of Mexico. Likewise, they separate the *L. nr. bocourti* population from the Pacific coast of Panama at a marked distance from the remaining samples, as would be expected given the lengthy closure of the Panamanian Isthmus; morphological study and taxonomic placement of this population within the eastern Pacific *L. bocourti/L. eiseni* complex is currently in progress (see Felder and Manning, 1998). Separation of the Colombian (Caribbean) *L. sinuensis* from the southwestern Gulf *Lepidophthalmus* sp. "a" is, while distinct ( $D_N = 0.16$ ), less marked than for other species and may reflect mutual relationships of these taxa to a common Caribbean stock. Not included in our analysis was the recently described *L. richardi* from Belize, which, on the basis of its ventral abdominal sclerotization and other morphological characters (Felder and Manning, 1997; Felder and Staton, 2000), appears to be the closest known relative of *Lepidophthalmus* sp. "a" from the southwestern Gulf of Mexico.

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