Systematic Relationships Among Florida Populations of *Argopecten irradians* (Lamarck, 1819) (Bivalvia: Pectinidae)

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ABSTRACT

Morphometric and genetic examinations (using allozyme electrophoresis) were conducted on two Florida populations of bay scallops, *Argopecten irradians* (Lamarck, 1819), to investigate the status of the subspecies *A. i. taylorae* Petuch, 1987. One other Florida population [*A. i. concentricus* (Say, 1822)] was examined morphometrically. Morphometric examinations emphasized mensural and meristic characters used in previous systematic diagnoses. Morphometric data were analyzed using analysis of variance and principal component analysis. Scallops taken from Florida Bay (putatively *A. i. taylorae* Petuch, 1987) were smaller but otherwise not morphologically distinct from populations of *A. i. concentricus* (Say, 1822) from Pine Island Sound and Homosassa Bay, Florida. Mean Nei's modified genetic distance value shows a close relationship between Florida Bay and Homosassa Bay scallops. Neither morphometric nor genetic evidence supports the proposed status of *A. i. taylorae* as distinct from Florida populations of *A. i. concentricus*.

Key words: Pectinidae, *Argopecten irradians*, morphometrics, systematics.

INTRODUCTION

Scallops are often distributed in patchy or contagious patterns, and, although disjunct local populations may be joined by variable degrees of larval exchange to form metapopulations (Levins, 1970; Andrewartha & Birch, 1984; Roughgarden *et al.*, 1985; Roughgarden & Iwasa, 1986; Simberloff, 1988; Hanski, 1989; Orensanz *et al.*, 1991), local populations along a species' range are probably self-sustaining (Sinclair *et al.*, 1985). Expectedly, reproductive isolation may contribute to genetic drift that can produce locally distinctive morphologies. The bay scallop, *Argopecten irradians* (Lamarck, 1819), which inhabits semi-enclosed coastal bays, sounds, and estuaries from Cape Cod, Massachusetts, to Tampico, Mexico (Clarke, 1965; Abbott, 1974), exemplifies the results of such isolation (Clarke, 1965; Waller, 1969; Kraeuter *et al.*, 1984).

Three extant subspecies of *A. irradians* have customarily been recognized: *Argopecten irradians irradians* (Lamarck, 1819), distributed from Cape Cod to New Jersey; *A. i. concentricus* (Say, 1822), distributed from New Jersey to South Carolina and from Palm Beach Inlet, Florida, to Louisiana; and *A. i. amplicostatus* (Dall, 1898), distributed from Texas into Mexico (Clarke, 1965; Waller, 1969, 1991; Abbott, 1974). A fourth subspecies, *A. i. sablensis* (Clarke, 1965), described from shells collected in Nova Scotia, apparently became extinct during the Holocene (Waller, 1969). These subspecies have been distinguished morphologically by plical number and shape, valve size and shape, and valve coloration (Clarke, 1965; Waller, 1969; Abbott, 1974). Bricelj *et al.* (1987), however, cautioned that subspecific distinctions within *A. irradians* have not yet been substantiated by biochemical techniques.

Recently Petuch (1987) described an additional subspecies of bay scallop, *Argopecten irradians taylorae*, based upon specimens from Rabbit Key Basin, Florida, and reported it to be restricted to Florida Bay and the western sides of the middle and upper Florida Keys (figure 1). Petuch (1987) reported that plicae of *A. i. taylorae* were more numerous than those of the other subspecies and that plicae were lower, wider, and more flattened than in *A. i. concentricus*. The valves of *A. i. taylorae* were also said to be much smaller, more fragile, and much more colorful than those of *A. i. concentricus* (table 1).

To emphasize the geographic isolation of *Argopecten irradians taylorae*, Petuch (1987) gave the distributional

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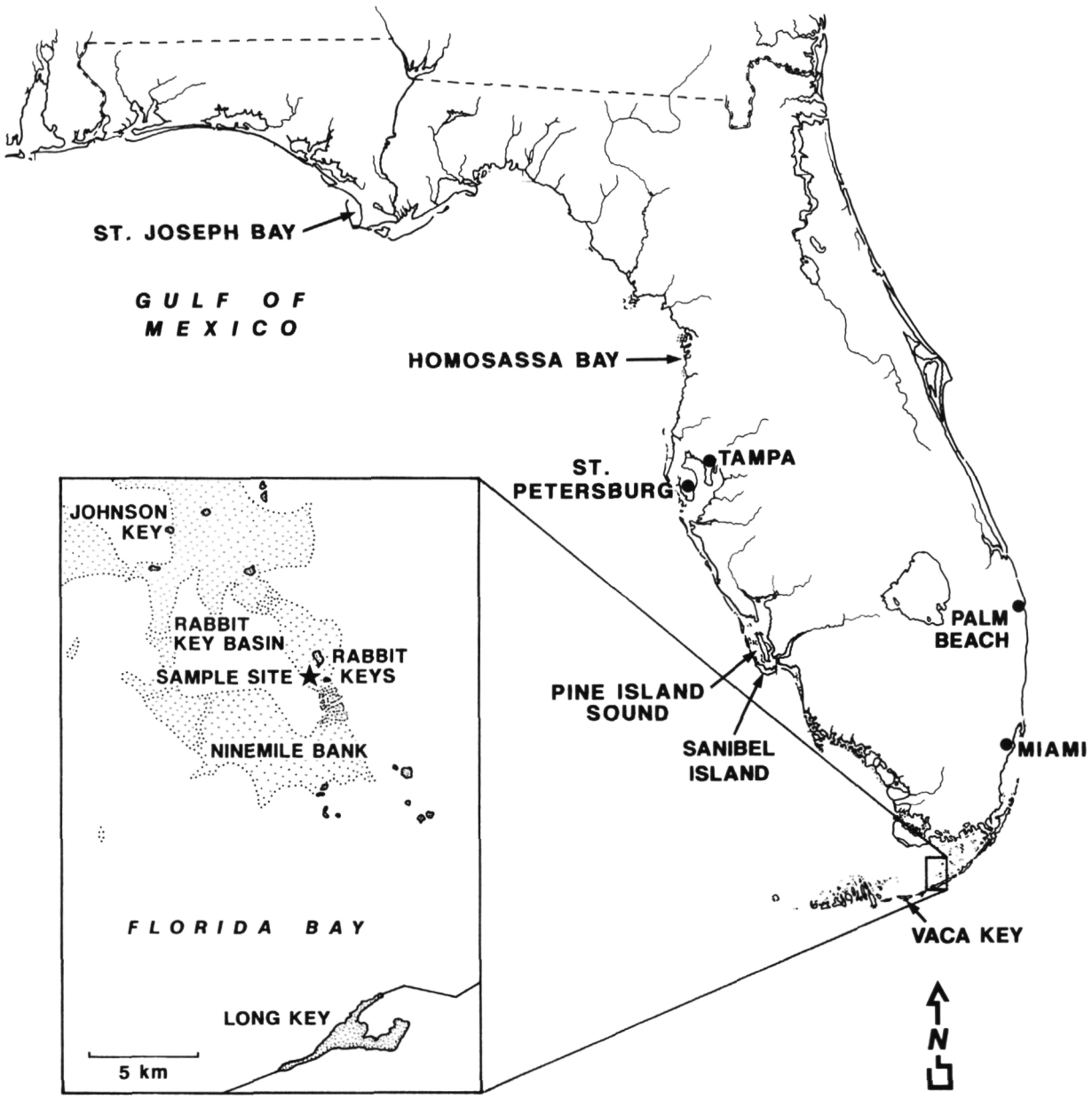


Figure 1. Florida: collecting locations of *Argopecten irradians* populations used in analyses and additional localities relevant to bay scallop populations. Inset shows location of collection within Rabbit Key Basin.

range of *A. i. concentricus* as "New Jersey to Georgia, and. . .Tampa, Florida to Louisiana." In doing so, he overlooked earlier Florida records of bay scallops at Boca Grande and Sanibel Island (Clarke, 1965); at Whitewater Bay, Sandy Key Basin, and south of Flamingo in Florida Bay (Tabb & Manning, 1961); and at several locations from Vaca Key in the middle Keys northward through Biscayne Bay to Palm Beach Inlet on the Florida east coast (Waller, 1969). Clarke (1965) and Waller (1969) had previously reported specimens from all of these locations as *A. i. concentricus,* but at least some of the specimens came from within the range of *A. i. taylorae.*

An investigation of the systematic status of *Argopecten irradians taylorae* was prompted by the need to address resource management issues. Bay scallops have historically supported small-scale commercial fisheries at various locations between Pensacola Bay and Pine Island Sound along Florida's west coast. Although the commercial fishery has decreased substantially in recent years, the species continues to be the target of an important recreational fishery throughout much of that region (Arnold, 1990). The presence of an isolated subspecies of bay scallop in Florida Bay, as reported by Petuch (1987), could have ramifications for resource management. The

Table 1. Characters of subspecies of *Argopecten irradians* reported by previous authors.

Subspecies	Clarke, 1965	Waller, 1969	Abbott, 1974	Petuch, 1987
Argopecten irradians irradians	16–20 (usually 16–18 ribs; ribs rounded; valve length and height nearly equal, L/H ratio approx. 1.06; W/H ratio approx. 0.21 (left) and 0.24 (right); right valve color as in Abbott (1974) but commonly white (or nearly so).	15–20 ribs; ribs low and rounded; L ≈ H; valves thinner and flatter and ribs lower than *A. i. concentricus*.	17–18 ribs; ribs low and roundish; valves most compressed of the 3 subspecies; right valve color only slightly lighter than left.	
Argopecten irradians concentricus	17–23 ribs; ribs rounded or with flattened tops; L/H ratio approx. 1.03 (l) and 1.02 (r); valves somewhat inflated, W/H ratio approx. 0.26 (l) and 0.32 (r); 75–100% of specimens with white or nearly white right valves, color otherwise like left valve except lighter.	15–22 ribs; ribs high, sharply rounded, becoming semi-hexagonal distally; differs from *A. i. irradians* by having thicker and more convex valves and higher ribs; differs from *A. i. amplicostatus* by having thinner and less convex valves.	19–21 ribs; ribs squarish; right valve much more convex than left; right valve lightest in color of the subspecies, commonly all white.	
Argopecten irradians amplicostatus	12–18 (usually 14–16) ribs; ribs rounded to slightly flattened; L/H ratio approx. 1.0 (l) and 1.01 (r); shell more inflated than other 2 subspecies, W/H ratio approx. 0.29 (l) and 0.34 (r); color of right valves usually white, sometimes with slight color tinge.	13–17 ribs; ribs high, sharply rounded proximally, becoming low and trapezoidal to semi-hexagonal distally; differs from *A. i. concentricus* by having thicker, more convex valves with fewer ribs.	12–17 ribs; right valve with high, squarish ribs; shell more gibbose than other subspecies; right valve commonly white.	
Argopecten irradians taylorae				23–25 ribs; ribs flatter and wider when compared with *A. i. concentricus*; shell smaller, more fragile and more colorful than *A. i. concentricus*; right valve generally yellow rather than white, with more brown mottlings than *A. i. concentricus*.

population might require separate management because of the increasingly popular recreational fishery or might require protection as a rare and isolated subspecies.

We used both allozyme electrophoresis and morphometric analyses to investigate the relationship of the Florida Bay population of *Argopecten irradians taylorae* to the Homosassa Bay population of *A. i. concentricus*. Valve characters were analyzed morphometrically for two Florida populations of *A. i. concentricus* and one of *A. i. taylorae*, as well as for the type series of *A. i. taylorae*.

Although subspecific morphometric variation within *A. irradians* has been investigated in other studies (Clarke, 1965; Waller, 1969), no effort had been made to characterize corresponding genetic variation. This study is the first to examine both morphological and genetic variation within a putative subspecies of *Argopecten irradians*.

MATERIALS AND METHODS

Bay scallops (n = 66) were collected from Rabbit Key Basin, the type locality of *Argopecten irradians taylorae*, on 29 August 1990. The scallops were located in the southeastern portion of the basin, in a turtle grass (*Thalassia testudinum* Banks ex König) bed, at a depth of approximately 2 m. At that time we also collected empty valves (n of right valves = 13) of *A. i. taylorae* from that locality. Scallops were returned to the Florida Department of Environmental Protection's Keys Marine Laboratory on Long Key, where sections of adductor muscle and mantle tissue were dissected from live animals and stored in liquid nitrogen for subsequent genetic analysis. Shells were disarticulated, numbered, and returned to the Florida Marine Research Institute at St. Petersburg. Additional samples of bay scallops were collected from Homosassa Bay (n = 60), just west of the mouth of the Homosassa River, on 24 July 1990 and from Pine Island Sound (n = 56) on 28 June 1991. The specimens from Homosassa Bay and Pine Island Sound were also collected from shallow ($z \leq 2$ m) *T. testudinum* beds; Homosassa Bay scallops were also examined both genetically and morphometrically, but Pine Island Sound scallops were examined only morphometrically.

Electrophoresis. Tissue samples of scallops from Homosassa Bay and Rabbit Key Basin were analyzed for genetic composition using methods reported in Bricelj and Krause (1992). Eight polymorphic loci (frequency of the most common allele ≤ 0.99) were examined, representing the following enzymes: phosphoglucomutase (PGM, EC 2.7.5.1), glucose-6-phosphate isomerase (GPI, EC 5.3.1.9), octopine dehydrogenase (ODH, EC 1.5.1.11), superoxide dismutase (SOD-1, EC 1.15.1.1), α-amino acyl peptide hydrolase (LAP, EC 3.4.1.-), alanyl aminopeptidase (AAP, EC 3.4.1.-), dihydrolipoamide dehydrogenase (DHLD, EC 1.8.1.4), and nonspecific aminopeptidase (AP, EC 3.4.1.-). SOD-1 was only weakly polymorphic (three alleles, $\bar{H} = 0.03$), and DHLD was inconsistently resolved; thus these two loci were not included in the data analysis.

The following enzymes examined were monomorphic: superoxide dismutase (SOD-2), β-galactosidase (β-GAL, EC 3.2.1.23), isocitrate dehydrogenase (two loci, IDH-1 and IDH-2, EC 1.1.1.42), mannose phosphate isomerase (MPI, EC 5.3.1.8), 6-phosphogluconate dehydrogenase (PGD, EC 1.1.1.44), catalase (CAT, EC 1.11.1.6), glycerol-3-phosphate dehydrogenase (GPDH, EC 1.1.1.8), triose phosphate isomerase (TPI, EC 5.3.1.1), esterase (two isozymes, EST-1 and EST-2, EC 3.1.-.-), arginine kinase (ARK, EC 2.7.3.3), L-iditol dehydrogenase (IDDH, EC 1.1.1.14), and malic dehydrogenase isozymes (MDH-1 and MDH-2, EC 1.1.1.37).

Alleles were designated using standard notation: the most common allele at each locus was assigned a value of 100 and other alleles were defined based on mobility relative to the most common allele.

Observed genotypic frequencies were compared with those expected under Hardy-Weinberg equilibrium using the G-test and, when necessary, Williams' correction for small sample size (Sokal & Rohlf, 1981). Rare alleles were pooled with the electrophoretically closest common allele to obtain genotypic class frequencies >5. Heterozygote deficit or excess was determined from the D statistic where D is the percentage deficit (Selander, 1970); negative D values indicate a deficit of heterozygous genotypes. Allele frequencies among populations were compared using the R × C test of independence and the G-test (Sokal & Rohlf, 1981). Nei's modified genetic distance (Nei, 1978) was calculated for each population pair surveyed.

Morphometrics. Morphological characters of scallops in populations from Homosassa Bay, Pine Island Sound, and Rabbit Key Basin and of the holotype (USNM 859901) and paratypes (USNM 859902) of *Argopecten irradians taylorae* were examined following the methods of Waller (1969). We also collected and examined a sample of recently emptied valves of scallops (putatively *A. i. taylorae*) from Rabbit Key Basin that appeared morphologically identical to living scallops from that area. For each scallop we counted right valve plicae and measured plical height, plical width, and 13 other valve characters dimension that have been applied in morphological comparisons of bay scallops (Clarke, 1965; Waller, 1969; Abbott, 1974; Petuch, 1987) (Appendix 1).

Mensural characters used by Petuch (1987) in his diagnosis were examined using analysis of variance (ANOVA) for their relationship to valve size in the same four populations. Data from the type series of *A. i. taylorae* from Rabbit Key Basin were deleted from the analyses of population effects because of the small sample size (n = 9) and the resultant undue influence on the statistical models.

Principal component analysis (PCA) was performed using only mensural variables. Marcus (1990) suggested that measurement error can unduly influence variability in the PCA model, so standard errors of measurement were calculated for each mensural character to estimate measurement error. Each character was measured 10 times on each of six specimens, two from each population, and standard errors were calculated for each specimen-by-character combination. Standard errors were then expressed as a percentage of the mean. Using all fifteen variables we log transformed ($\log_{10}$) the values and performed a standard PCA (PRINCOMP procedure, SAS Institute, Inc., 1985). Burnaby's (1966) method of size-corrected PCA was performed separately on all data [size-corrected PCA (N. Macleod, personal communication)]. Burnaby's method removes most of the influence of size on the PCA by constructing variables orthogonal

Table 2. Allele frequencies for polymorphic enzymes from populations of *Argopecten irradians* from Rabbit Key Basin and Homosassa Bay, Florida. n = number of alleles sampled (2 × number of individuals). N_e = effective number of alleles (after Hartl & Clark, 1989).

		Frequency	
Locus	Allele	RKB	HOM
AP	108	0	0.02
	104	0.38	0.23
	100	0.53	0.51
	96	0.08	0.24
	94	0.01	0
	n	132	118
	N_e	2.32	2.70
AAP	102	0	0.03
	100	0.35	0.40
	98	0.17	0.24
	97	0.13	0.04
	96	0.19	0.17
	94	0.15	0.13
	n	132	112
	N_e	4.37	3.79
LAP	100	0.62	0.85
	96	0.37	0.15
	94	0.01	0
	n	132	118
	N_e	1.92	1.35
ODH	106	0.01	0.02*
	104	0.08	0.13
	102	0	0.01
	100	0.77	0.80
	96	0.07	0
	94	0.01	0.04
	90	0.05	0
	n	132	118
	N_e	1.63	1.52
PGM	98	0.02	0.01*
	96	0.49	0.56
	95	0.14	0.18
	94	0.13	0.19
	92	0.11	0.01
	91	0.03	0
	90	0.07	0.05
	n	132	118
	N_e	3.36	2.61
GPI	150	0	0.01
	106	0.06	0.02
	104	0.61	0.62
	100	0.30	0.33
	99	0.02	0.01
	98	0.01	0
	n	132	118
	N_e	2.14	2.02

* Genotype frequencies not in Hardy-Weinberg equilibrium.

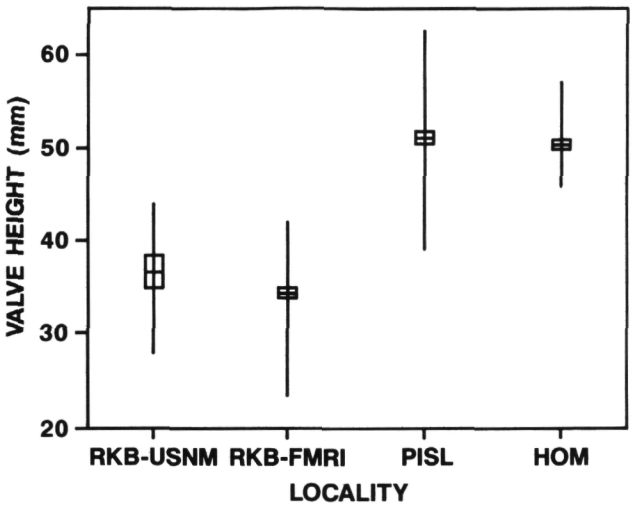


Figure 2. Valve heights of Florida Gulf coast *Argopecten irradians* populations. Plots show mean, range, and ± 1 standard error. RKB-USNM: Rabbit Key Basin, type series of *Argopecten irradians taylorae*, USNM 859901 & 859902; RKB-FMRI: Rabbit Key Basin, collection made for this study, FSBC I 41441; PISL: Pine Island Sound, FSBC I 44439; HOM: Homosassa Bay, FSBC I 40337.

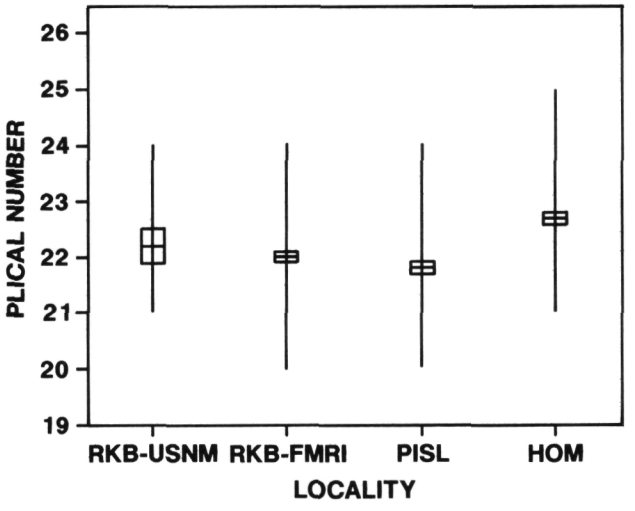
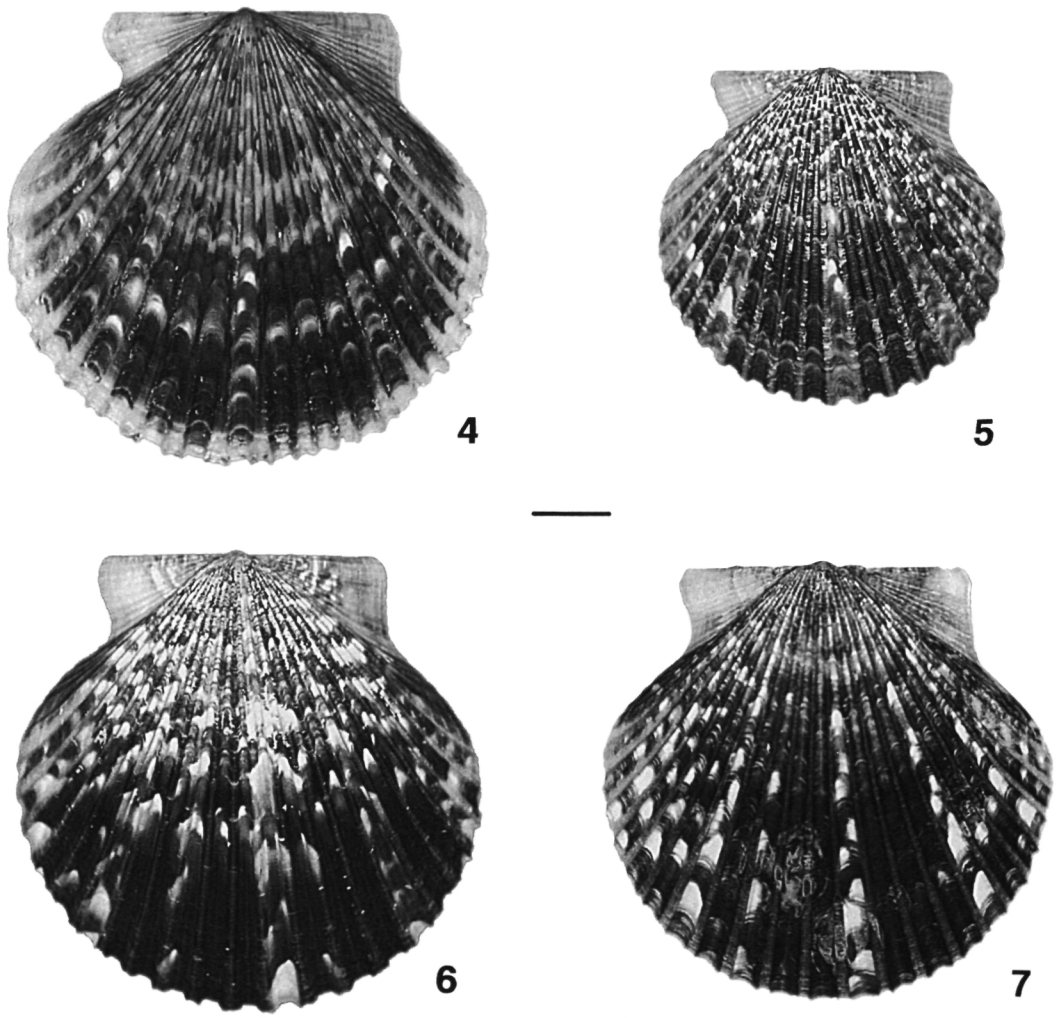


Figure 3. Numbers of right valve plicae for Florida Gulf coast *Argopecten irradians* populations. Plots show mean, range, and ± 1 standard error. RKB-USNM: Rabbit Key Basin, type series of *Argopecten irradians taylorae*, USNM 859901 & 859902; RKB-FMRI: Rabbit Key Basin, collection made for this study, FSBC I 41441; PISL: Pine Island Sound, FSBC I 44439; HOM: Homosassa Bay, FSBC I 40337.

to a variable that is considered to represent size (Rohlf & Bookstein, 1987). The relative contribution of each variable to the variation represented by PC2 and PC3 was determined, and Cattell's (1966) scree test was used to identify and eliminate variables that failed to add substantially to the variance in the analysis, leaving 9 variables: AM, AD, DG, AK, GP, BJ, IW, ad, and ce (see Appendix 1 for explanations). Using only these variables, data were reanalyzed, and size-adjusted shape variation among populations was examined using PC2 and PC3 generated by the Burnaby technique.



Figures 4–7. Left valves of *Argopecten irradians* from Florida. **4.** *A. i. concentricus*, height 60.0 mm, Rabbit Key Basin, FSBC I 41441. **5.** *A. i. taylorae*, holotype, height 44.0 mm, Rabbit Key Basin, USNM 859901. **6.** *A. i. concentricus*, height 60.1 mm, Homosassa Bay, FSBC I 40337. **7.** *A. i. concentricus*, height 57.9 mm, Pine Island Sound, FSBC I 44439. Scale bar = 10 mm.

Growth relationships of valve characters within and between populations were examined using the method of Jolicoeur (1963). Eigenvectors (coefficients) of PC1 from the standard PCAs using log-transformed data for all populations combined and separately on populations from the three localities were compared with $(1/p)^{0.5}$, where p = the number of variables and therefore $(1/p)^{0.5} = 0.333$. Coefficients for valve characters that varied above or below 0.333 represented factors that reflected positive or negative allometry.

Valve color and pattern were examined following the criteria of Elek and Adamkewicz (1990), with the exception that the relationship between color pattern and population was examined using the nonparametric Kruskal-Wallis procedure.

Disposition of specimens: Except for the type material of *Argopecten irradians taylorae*, valves of all specimens examined have been deposited in the Florida Marine Research Institute Invertebrate Collection, lot numbers FSBC I 40337 (Homosassa Bay), FSBC I 41441 (Rabbit Key Basin), and FSBC I 44439 (Pine Island Sound).

RESULTS

Electrophoresis. Among the polymorphic loci no significant differences were found between populations for the loci GPI, ODH, AAP, or PGM. Allele frequencies between Homosassa Bay and Rabbit Key Basin populations were significantly different for amino peptidase (AP, $p < 0.05$) and leucine amino peptidase (LAP, $p < 0.001$) (table 2).

The mean percentages of heterozygous loci per individual (MLH) for Homosassa Bay and Rabbit Key Basin populations were 43% and 44% using the six polymorphic loci. Homosassa Bay scallops fit Hardy-Weinberg expectations for heterozygosity at all loci, but the Rabbit Key Basin population had heterozygote deficits at the PGM ($p < 0.05$) and ODH ($p < 0.01$) loci.

Table 3. Growth relationships for valve characters from Rabbit Key Basin (RKB), Pine Island Sound (PISL), and Homosassa Bay (HOM), Florida *Argopecten irradians* populations analyzed using principal component analysis. Numbers are eigenvectors of principal component 1 and indicate positive or negative allometric growth where eigenvectors vary above or below $1/\sqrt{p}$, where p = the total number of characters, following Jolicoeur (1963).

Character	Population			
	All populations	RKB	PISL	HOM
AM	0.3132	0.3157	0.3265	0.1672
AD	0.3037	0.3095	0.3385	0.1447
DG	0.3087	0.3340	0.2589	0.2415
AK	0.3063	0.6240	0.3139	0.2051
GP	0.3302	0.3212	0.4259	0.1548
BJ	0.2635	0.3348	0.3178	0.2051
IW	0.0796	0.2789	0.3457	0.5943
ad	0.3696	0.3301	0.3739	0.4236
ce	0.5469	0.4313	0.2675	0.5015

The mean genetic distance between the Homosassa Bay and Rabbit Key Basin populations was 0.035.

Morphometrics. Standard error estimates for measurements of morphometric characters were universally low, averaging 0.64% of the mean for all variables, suggesting that measurement error did not overly influence the variance in subsequent morphometric analyses.

Scallops from the Pine Island Sound collection were significantly larger than those from Homosassa Bay, and both Pine Island Sound and Homosassa Bay scallops were much larger than those from our Rabbit Key Basin collection (ANOVA, all $p < 0.05$) (figures 2–3). The type specimens of *Argopecten irradians taylorae* were slightly larger than the live specimens from our Rabbit Key Basin collection and similar in size to the empty valves we collected from Rabbit Key Basin, although two pairs of empty valves exceeded 50 mm in height. Representative valves from the sample populations are illustrated in figures 4–7.

Numbers of right-valve plicae were similar for all sample populations that we examined morphometrically, and plical number was not significantly related to valve height ($0.05 < p < 0.06$). However, the effect of population on plical number was significant ($p < 0.0001$), and right-valve plicae were significantly more numerous on Homosassa Bay scallops ($p < 0.05$) than on Rabbit Key Basin and Pine Island Sound scallops. Plical numbers were not significantly different between Rabbit Key and Pine Island Sound populations. Width of plicae relative to valve size was positively related to valve height ($p < 0.0002$).

Patterns of growth for individual mensural characters varied greatly and inconsistently among populations (table 3). Although some characters varied isometrically, there was no consistent trend among populations.

Coloration of valves from all populations was similar; more than 90% of specimens from each population exhibited the color pattern of type E of Elek and Adamkewicz (1990). Variations in color pattern were not significantly different among populations. More than 95% of the valves from each scallop population had white backgrounds, and 100% of the specimens had mottled left valves (table 4). Excluding one yellow and two orange scallops from Rabbit Key Basin and one orange scallop from Pine Island Sound, right valves in all populations were consistently all white except in the early juvenile region of the shell.

The first principal component (PC1) from the standard PCA of all data accounted for 83.3% of the total variance, and the second and third principal components accounted for 7.7% and 4.1%, respectively, of the variance. Burnaby size-corrected PCA showed that principal components 1 through 3 accounted for 59.2%, 14.9%, and 9.8% of total variance, respectively. Two variables in the Burnaby PCA accounted for most of the variance in PC2 and PC3: width of plical interspaces (IW) represented 28.5% of PC2 variance and 69.5% of PC3 variance, and ce (length of ligament insertion) accounted for 33.6% of PC2 variance and 20.4% of PC3 variance (table 5). Plots of PC2 and PC3 from the size-corrected PCA of the data from all 3 populations and including the separate collection of empty valves from Rabbit Key Basin (figure 8) demonstrate that scatterplots from each population overlap with those from all other populations. Particularly extensive overlap occurs between the Rabbit Key Basin and Homosassa Bay populations, and less overlap is seen in plots representing the Pine Island Sound population and those of all other populations.

DISCUSSION

The genetic distance (D = 0.035) between the Homosassa Bay and Rabbit Key Basin populations of *Argopecten*

Table 4. Summary of color and color pattern on valves of *Argopecten irradians* from Rabbit Key Basin (RKB, n = 66), Pine Island Sound (PISL, n = 56), and Homosassa Bay (HOM, n = 60), Florida. Numbers expressed as percentages.

Population	Background color			Rays present		Mottling		Banding	
	White	Yellow	Orange	Left	Right	Left	Right	Left	Right
RKB	95.5	1.5	3.0	90.9	30.3	100	80.3	100	57.6
PISL	98.2	0	1.8	96.4	12.5	100	85.7	41.1	58.9
HOM	100	0	0	98.3	6.7	100	93.3	98.3	90.0
MEAN	97.8	0.5	1.6	95.1	17.0	100	86.3	81.3	68.7

Table 5. Percentage of variance in principal components 2 and 3 from Burnaby PCA attributable to individual valve characters for *Argopecten irradians* populations from Rabbit Key Basin, Pine Island Sound, and Homosassa Bay. Character abbreviations are defined in the appendix.

Character	Principal component 2	Principal component 3
AM	4.78	1.13
AD	3.60	1.73
DG	2.09	0.72
AK	6.86	2.28
GP	9.18	3.09
BJ	8.13	0.20
IW	28.50	69.50
ad	3.28	0.89
ce	33.57	20.43

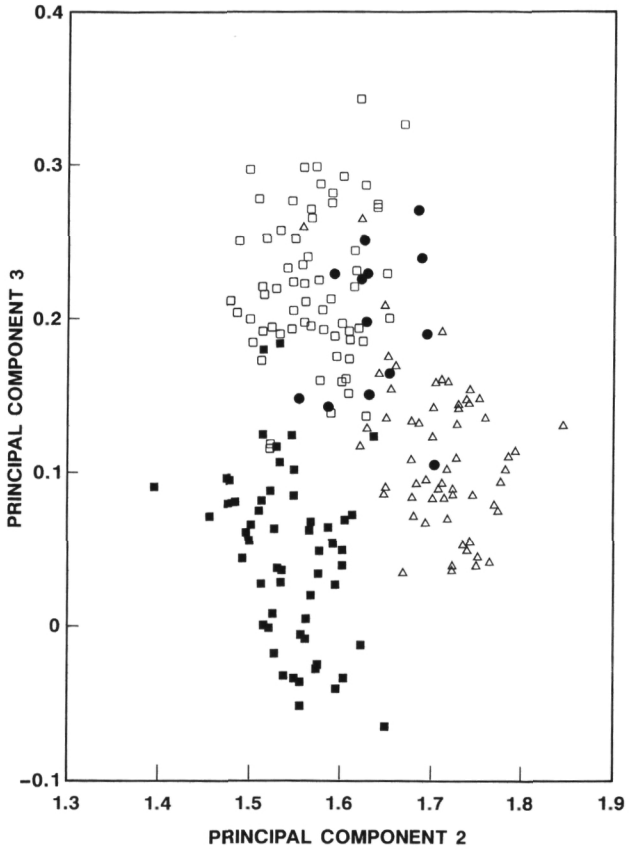


Figure 8. Bivariate scatterplot of principal component 2 and 3 scores generated using Burnaby's (1966) size-corrected principal component analysis on morphometric measurements of *Argopecten irradians* from Rabbit Key Basin (□), Pine Island Sound (■), and Homosassa Bay (△) populations. Population indicated by (●) represents empty valves collected from Rabbit Key Basin locality.

irradians s.l. is on the order of distances between local races (Nei, 1976, 1987). This value is comparable to those between disjunct but apparently recently separated populations of the Baltic clam *Macoma balthica* (Linnaeus, 1758) (Nei's D = 0.058) (Meehan *et al.*, 1989) and between Great Barrier Reef and Enewetak Atoll populations of the giant clam *Tridacna maxima* (Nei's D = 0.033) (Ayala, 1975). Electrophoretic data from five additional populations of *Argopecten irradians s.l.* examined by Krause (1992) (Martha's Vineyard, Massachusetts; Niantic River, Connecticut; Orient Harbor, Long Island, New York; Core Banks, North Carolina; and St. Joseph Bay, Florida), treated identically, were used along with data from the Rabbit Key Basin and Homosassa Bay populations to create a genetic distance matrix. A dendrogram was constructed from the genetic distance matrix using the unweighted pair-group method with arithmetic mean (UPGMA Sneath & Sokal, 1973), provided by the computer program NTSYS (Applied Biostatistics, Inc.) (figure 9). Standard errors of tree branching points were estimated using the procedure of Nei *et al.* (1985) who point out that, when using electrophoretic data and less than 30 loci, the topology of a reconstructed tree is subject to a large stochastic error. The size of the errors allows us little confidence in the dendrogram, but two factors may contribute to an inflation of the estimated standard errors. When genetic distance values are very low, less than 0.105, the value of I in the equation $D = -\log_e I$ exceeds 0.9. When $I > 0.9$ and average heterozygosity (MLH) is >0.2 serious overestimation of the variance may occur (Nei *et al.*, 1985). Twelve of 21 pairwise I values in the scallop genetic distance matrix exceed 0.9 and MLH = 0.44 p. Despite the size of the standard errors, the genetic distance data indicate a close relationship between the Rabbit Key Basin and Homosassa Bay scallops within *Argopecten irradians*.

The small but significant differences in allele frequency between Homosassa Bay and Rabbit Key Basin populations at the AP and LAP loci might be evidence for localized selection among genotypes between these sites (McMillen *et al.*, 1994), for reduced gene flow between the populations (Beaumont & Zouros, 1991), or some combination of these processes. The overall magnitude of genetic variation among the Florida populations is only slightly greater than that found among Krause's (1992) northern populations of *A. i. irradians*. Therefore *A. i. taylorae* appears, based on genetic evidence, not to differ at the subspecific level from other Florida populations examined.

Values for the mean percentage of heterozygous loci per individual (MLH) in the Homosassa Bay (43%) and Rabbit Key Basin (44%) populations are relatively high but similar to the 45.3% MLH reported by Bricelj and Krause (1992) for *Argopecten irradians irradians* from the Niantic River estuary, Connecticut. These values indicate that high MLH values may be characteristic of *Argopecten irradians s.l.*, but Wall *et al.* (1976) reported a MLH of 11.6% for *A. irradians* from Bogue Sound, North Carolina. Values of MLH reported for 5 other pectinids range from 9.4% to 32.1% (Nikiforov & Dolgonov, 1982; Beaumont & Beveridge, 1984).

Color in *Argopecten irradians* is genetically controlled

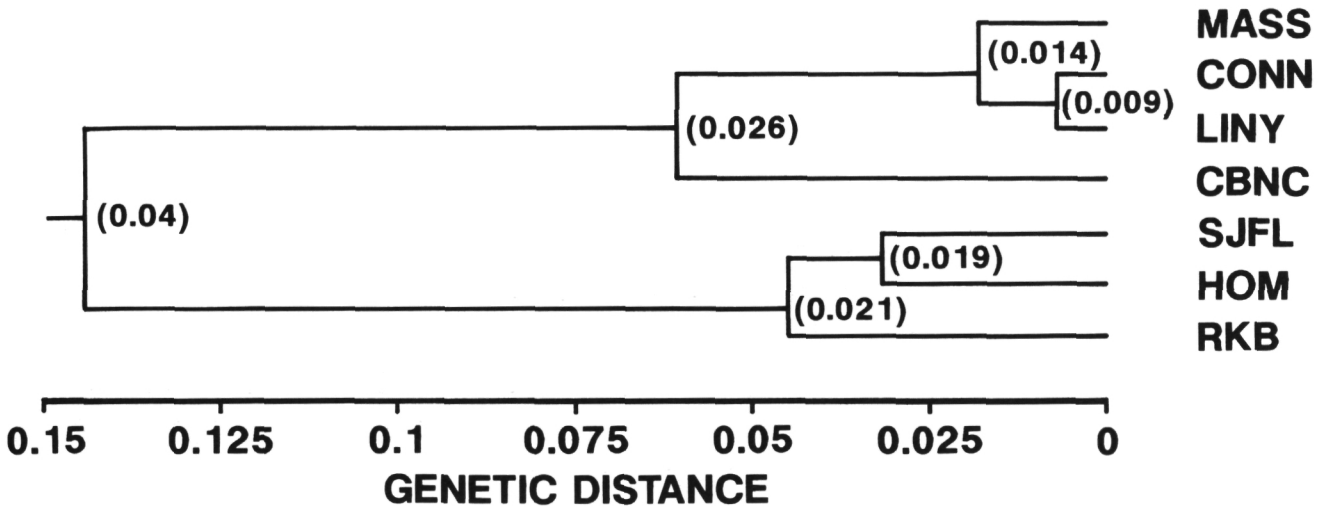


Figure 9. UPGMA tree constructed from the Nei (1972) genetic distance matrix for populations of *Argopecten irradians*. Population abbreviations are MASS: Martha's Vineyard, Massachusetts; CONN: Niantic River, Connecticut; LINY: Orient Harbor, Long Island, New York; CBNC: Core Banks, North Carolina; SJFL: St. Joseph Bay, Florida; HOM: Homosassa Bay, Florida; RKB: Rabbit Key Basin, Florida. Numbers in parentheses are standard errors of branching points estimated using the procedure of Nei *et al.* (1985).

and may sometimes be useful in distinguishing individuals and populations (Kraeuter *et al.*, 1984; Adamkewicz & Castagna, 1988). Nevertheless, we found no substantial differences in valve coloration or color pattern between the Homosassa Bay, Pine Island Sound, and Rabbit Key Basin scallop populations to support Petuch's (1987) contention that shells of *A. i. taylorae* are much more colorful than those of *A. i. concentricus*. Most scallops in each of the populations had a rayed pattern on the left valve, and additional color was generally expressed as mottling and banding, somewhat obscuring the rayed pattern. Variations in the intensity of color were affected by the nature and extent of fouling on the left valve and possibly by ontogenetic change.

Petuch (1987) identified the small size of scallops from the Rabbit Key Basin population as an important character that distinguishes *Argopecten irradians taylorae* from *A. i. concentricus*. Although heights of live scallops from our Rabbit Key Basin collection were significantly smaller than those in all other collections, the empty valves that we collected from the same locality were comparable in size to those in Petuch's type series. This suggests that the scallops in Rabbit Key Basin may indeed be distinctively smaller than other Florida scallops, although the close genetic similarity between the Rabbit Key Basin and Homosassa Bay populations indicates that scallop size is readily influenced by local conditions. The small size of our live Rabbit Key Basin collection coupled with the heterozygote deficits at the loci ODH and PGM that occurred among the scallops from this collection [similar to deficits at these loci that have been reported for juveniles of other species of Pectinidae (Volckaert & Zouros, 1989; Bricelj & Krause, 1992)] may indicate that the scallops we collected from Rabbit Key Basin were juveniles.

Discontinuities in plical number occur between populations of *Argopecten irradians* along the geographic range of the species, and these differences have been emphasized taxonomically (Clarke, 1965). The number of plicae ranges from 12 to 25 in the described subspecies (Clarke, 1965; Waller, 1969; Abbott, 1974; Petuch, 1987) and is reportedly under genetic control (Kraeuter *et al.*, 1984). We substantiate the elevated plical numbers that have been reported for Florida *A. i. concentricus*, but we did not find even greater plical counts in the Rabbit Key Basin population as reported by Petuch (1987). In fact, the mean plical number for our sample of scallops from Rabbit Key Basin was statistically indistinguishable from that of scallops from Pine Island Sound. Higher counts of plicae for the type series reported by Petuch (1987) suggest that he may have misidentified as plicae some of the "riblets" that occur on the disk flanks of this species; such confusion has been previously reported by Clarke (1965) and Waller (1969). Our analysis of right valve plical numbers rejects the conclusion that scallops from Rabbit Key Basin represent a separate and unique subspecies.

Width of the plicae at the ventral margin was identified by Petuch (1987) as a character that can be used to separate *Argopecten irradians taylorae* from *A. i. concentricus*. However, because plical width relative to valve size is positively correlated with valve height, its use in a univariate comparison of scallops of different sizes without accounting for allometry is invalidated. Moreover, our data indicate that Rabbit Key Basin scallops have relatively narrower plicae than do scallops from Homosassa Bay or Pine Island Sound—not wider as reported by Petuch.

Inconsistencies in the relationship between growth and valve characters between populations indicate that morphometric characters do not vary with growth in a simple manner; variability due to small sample sizes and mea-

surement error may also affect the allometric coefficients (Marcus, 1990). Regardless of the source, the inconstancy of shape variables and the presence of allometric relationships among mensural characters, morphometric ratios, and size cast doubt upon the use of univariate characters in describing morphometric differences between scallop populations, adding empirical emphasis to warnings by previous authors (summarized in Humphries *et al.*, 1981).

Burnaby size-corrected PCA failed to distinctly separate the Rabbit Key Basin, Pine Island Sound, and Homosassa Bay scallop populations. Although morphometric overlap among populations is evident in the plots of PC2 and PC3, scatterplots of the individual populations form distinct clusters and indicate that the more geographically distant populations (Rabbit Key Basin and Homosassa Bay) in our samples were morphometrically more similar. Variation in shape, and hence some separation in the plots of PC2 and PC3, may be influenced by ontogeny of individuals, because the Burnaby technique does not completely remove the effect of size (Humphries *et al.*, 1981), but separation on the basis of shape variables indicates that scallop shape is heavily influenced by local conditions and may simply reflect ecophenotypic variation.

We assessed alleged differences between typical *Argopecten irradians taylorae* and representatives of other bay scallops from peninsular Florida. Based on the results of our electrophoretic and morphometric examinations, we refute those differences and conclude that bay scallops from Rabbit Key Basin do not represent a subspecific taxon distinct from Florida populations of *A. i. concentricus*.

ACKNOWLEDGEMENTS

Clarita Lund, Brenda Hedin, Richard Darden, Yantian Lu, Don Hesselman, and James Seagle assisted in collecting scallops, and C. Lund also performed data entry. Robert McWilliams and Charlotte LaTorre measured valve characters. Catherine Bray assisted in data analysis and figure preparation. Llyn French prepared figures. Dr. Theresa Bert and Héctor Cruz-López helped with interpretation of electrophoretic data. Everglades National Park biologist Daniel Foxen facilitated our Florida Bay collection. This project was partially supported by funds created by the Florida Saltwater Products License and the Florida Saltwater Fishing License. Electrophoretic analyses were supported by a National Science Foundation dissertation improvement grant (BSR–9015991) to MKK.

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APPENDIX I

Table of morphological characters and abbreviations used in this study, following Waller (1969). Abbreviations refer to either right or left-valve; apostrophes are added in text to indicate left valve measurements.

AM	Valve height
AD	Length of posterior portion of valve
DG	Length of anterior portion of valve
AK	Height of posterodorsal portion of valve
GP	Height of anterodorsal portion of valve
DF	Length of anterior ligament
CD	Length of posterior ligament
EI	Height of anterior auricle
BJ	Height of posterior auricle
DE	Length from valve midline to ventral insertion of anterior auricle
LO	Valve width
ad	Height of resilial insertion
ce	Length of resilial insertion
PW	Width of medial plicae at ventral margin
IW	Width of medial interplical spaces at ventral margin