Genetic and Morphological Divergence of a Circumtropical Complex of Goatfishes: *Mulloidichthys vanicolensis*, *M. dentatus*, and *M. martinicus*[1]

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ABSTRACT: Allozyme and meristic data were used to compare relationships among three species of a circumtropical complex of goatfishes that are very similiar in color and morphology: *Mulloidichthys vanicolensis* (Valenciennes) of the Indo-Pacific, *M. dentatus* (Gill) of the eastern Pacific, and *M. martinicus* (Cuvier) of the western Atlantic. The species are distinguished by several allozyme differences as well as by gill-raker counts. Allozyme data from several widely separated populations of *M. vanicolensis* (including isolated islands with high endemism in other groups) suggest little genetic divergence, consistent with high levels of dispersal and gene flow. Morphological data suggest greater divergence between populations of *M. vanicolensis* from the western Indian Ocean and the Pacific Ocean than is apparent from allozyme data.

THREE ALLOPATRIC NOMINAL species of goat-fishes of the genus *Mulloidichthys* Whitley (*Mulloides* Bleeker of some authors), *M. vanicolensis* (Valenciennes, 1831) of the tropical Indo-Pacific, *M. dentatus* (Gill, 1862) of the tropical eastern Pacific, and *M. martinicus* (Cuvier, 1829) of the tropical western Atlantic, are remarkably similar in general morphology and coloration, all being silvery white with a yellow lateral stripe and yellow median fins (Plate I). [Phillip C. Heemstra (pers. comm.) believed that Whitley was in error in proposing *Mulloidichthys* to replace *Mulloides* Bleeker, and some recent authors have followed his advice. Eschmeyer (1990), however, treated *Mulloidichthys* as a valid genus of Mullidae, and Heemstra has informed us that

he now agrees.] Morphological and genetic relationships of these species were reexamined in this study to determine if these approaches show similar levels and patterns of divergence. In addition, several widely separated populations of *M. vanicolensis*, including some from the isolated Hawaiian Archipelago and Easter Island, where many endemic fish species are found, were examined for possible differences.

Mulloidichthys martinicus and *M. dentatus* are one of the geminate pairs found on either side of the Isthmus of Panama. During the Miocene there was a broad channel across the Isthmus linking the western Atlantic Ocean and the eastern Pacific. This sea passage was closed in the Pliocene, resulting in the isolation of the tropical marine biota of the eastern Pacific from that of the Caribbean Sea. Recent estimates of the time that has elapsed since the emergence of the Panama land barrier have ranged from 1.8 (Keller et al. 1989) to 3.5 (Coates et al. 1992) million years. About a dozen species of shore fishes appear to be morphologically undifferentiated on either side of the isthmus (if circumtropical species are eliminated). Jordan (1885) noted that there are also many closely related pairs on each side, which he termed geminate species. These are presumed to have diverged since the eastern Pacific was isolated from the Atlantic. Systematists may differ as to whether the

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members of each of these pairs deserve to be recognized as species, but regardless of the taxonomic decisions, the level of differentiation can be documented.

Vawter et al. (1980) selected examples of geminate species and species for which no morphological differentiation had been demonstrated from each side of the Isthmus of Panama for a study of genetic differentiation using allozyme electrophoresis. Among the species pairs they chose was *M. martinicus* and *M. dentatus*. They found a level of genetic divergence that indicated species-level separation. In our study, morphometric and meristic data of the two are compared to determine if there is a similar level of morphological variation.

The third species of what we term the *martinicus* complex, *M. vanicolensis*, ranges from the Red Sea and east coast of Africa to the easternmost islands of Oceania. Some authors, including Lachner (*in* Schultz and collaborators [1960]), have referred to this species as *Mulloidichthys auriflamma* (Forsskål, 1775), but Klausewitz and Nielsen (1965) examined Forsskål's type specimen of *Mullus auriflamma* and determined that it is not a species of *Mulloidichthys*.

The primary objective of this study was to examine the degree of genetic and morphological divergence between *M. vanicolensis* and *M. dentatus*, and to determine whether there is significant variation in *M. vanicolensis* along its vast range from East Africa to Hawaii and Easter Island. This study is preliminary to a revision of the mullid genera *Mulloidichthys* and *Parupeneus* in preparation by J.E.R.

MATERIALS AND METHODS

Morphological Data

Meristic and morphometric data were taken from museum specimens of the three species of *Mulloidichthys* of the *martinicus* complex. The following morphometric measurements were made by J.E.R.: standard length (SL), body depth, snout length, orbit diameter, barbel length, pectoral-fin length, and pelvic-fin length. The median fins of museum specimens of this genus are often broken at the distal ends, making accurate measurements difficult. Preliminary measurements of these fins also did not offer any promise of significant differences. Number of upper and lower gill rakers was determined. Analysis of variance (ANOVA) tests (Sokal and Rohlf 1981) were done on differences among the three species and between Indian and Pacific Ocean populations of *M. vanicolensis*.

Enzyme Electrophoresis

Specimens of *M. vanicolensis* were collected by J.E.R. either by spearing or from fish markets, including 12 from the Hawaiian Islands, 2 from Guam, 1 from Tahiti, 2 from Easter Island, and 5 from Oman in the Indian Ocean (Figure 1). Tissues from 20 specimens of *M. dentatus* from Los Islotes, near Isla Partida in the cape region of Baja California Sur, Gulf of California, Mexico, were collected by R.H.R. from speared fish. Tissue samples were immediately frozen and transported to the Scripps Institution of Oceanography (S.I.O.), where they were stored at $-40°C$. Sampled specimens from the Indo-Pacific are deposited at the Bernice P. Bishop Museum in Honolulu, Hawaii.

Separate extracts of eye, liver, and muscle were prepared from each specimen. Tissues were homogenized in a $1:1$ volume:volume mixture of tissue and 0.1 M potassium phosphate grinding buffer (pH 7 [Waples and Rosenblatt 1987]) and centrifuged at 20,000 × g for 10 min. The supernatant fraction was then subjected to horizontal starch electrophoresis in 12.5% starch gels (Sigma starch; Sigma Chemical Co., St. Louis, Missouri 63178). The enzymes and tissues surveyed, loci scored ($n = 42$), and buffer solutions used are listed in Table 1. Staining methods and recipes were adapted from Selander et al. 1971, Waples 1986, Buth and Murphy 1990, and Stepien and Rosenblatt 1991. Enzyme nomenclature follows recommendations of the International Union of Biochemistry (1984) and Shaklee et al. (1990). Relative migration distances were compared with the most com-
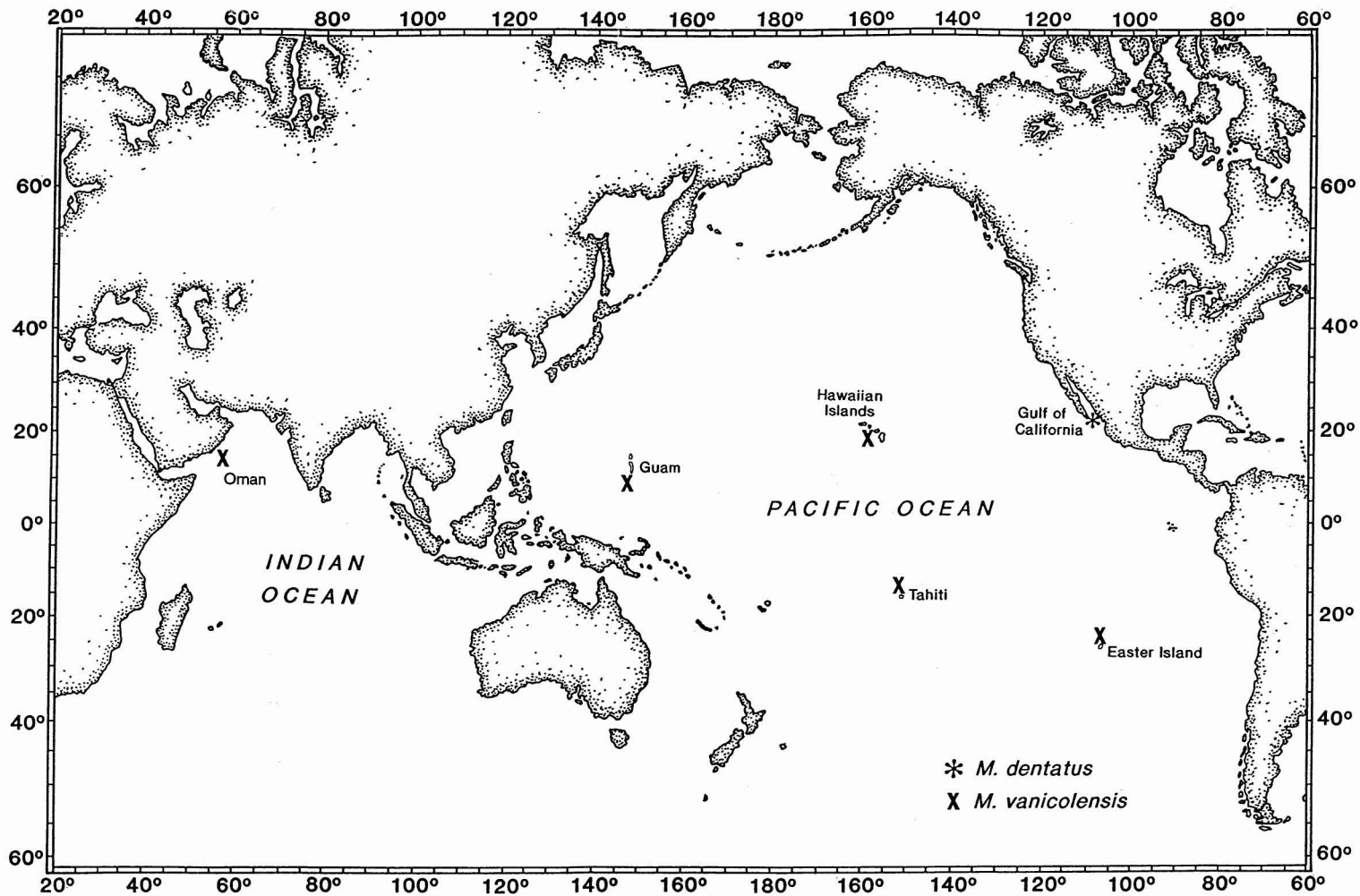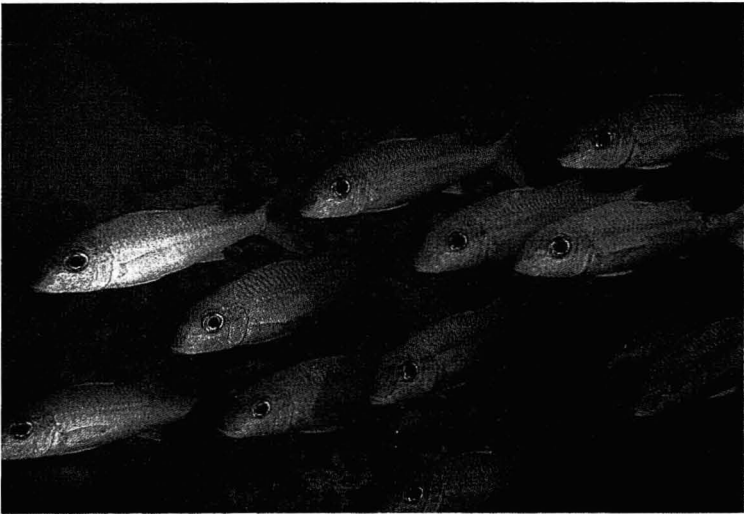
FIGURE 1. Map showing populations sampled for allozyme study.

PLATE I. Species of the *Mulloidichthys martinicus* complex, A, *M. martinicus;* B, *M. vanicolensis;* C, *M. dentatus.* (Photos, J. Randall.)

TABLE 1

ENZYMES SURVEYED IN ELECTROPHORETIC ANALYSES

NAME (E.C. NUMBER)	LOCUS	TISSUE[a]	BUFFER[b]
Acid phosphatase (3.1.3.2)	ACP-1*	L	1
	ACP-2*	L	1
Aconitase hydratase (4.2.1.3)	sAH-1*	L	1
	mAH-2*	L,M	1
Adenylate kinase (2.7.4.3)	AK*	M	1,2
Alcohol dehydrogenase (1.1.1.1)	ADH-1*	L	2,3
	ADH-2*	L	2,3
Aspartate aminotransferase (2.6.1.1)	sAAT-1*	L	1,2
	sAAT-2*	M	1,2
	mAAT*	L,M	1,2
Creatine kinase (2.7.3.2)	CK-B*	E	2
	CK-C*	L	1,2
	CK-A*	M	1,2
Esterase (3.1.1.-)	EST-1*	L,M	4
	EST-2*	L,M	4
Fumarate hydratase (4.2.1.2)	FH*	L	1,2
Glucose-6-phosphate dehydrogenase (1.1.1.49)	G6PDH-1*	L	2,3
	G6PDH-2*	L	2,3
Glucose-6-phosphate isomerase (5.3.1.9)	GPI-1*	E,L,M	2,4
	GPI-2*	M,E	2,4
Glutamate dehydrogenase (1.4.1.2)	GLUDH*	L,M	1
Glyceraldehyde-3-phosphate dehydrogenase (1.2.1.12)	GAPDH-1*	E,L	1,2
	GAPDH-2*	M	1,2
Glycerol-3-phosphate dehydrogenase (1.1.1.8)	G3PDH-1*	L,M	1,2
	G3PDH-2*	M	1,2
L-Iditol dehydrogenase (1.1.1.14)	IDDH*	L	1
Isocitrate dehydrogenase (NADP) (1.1.1.42)	sIDHP*	E,L	1,2
	mIDHP*	E,M	1,2
L-Lactate dehydrogenase (1.1.1.27)	LDH-C*	E	1,2
	LDH-A*	E,M	1,2
	LDH-B*	E,L	1,2
Malate dehydrogenase (1.1.1.37)	sMDH-B*	M	1,2
	sMDH-A*	L	1,2
Mannose-6-phosphate isomerase (5.3.1.8)	MPI*	L,M	2
Phosphoglucomutase (5.4.2.2)	PGM-1*	L,M	1,2
	PGM-2*	M	1,2
Phosphogluconate dehydrogenase (1.1.1.44)	PGDH*	M	1
Peptidase A (glycyl-l-leucine) (3.4.11.-)	PEPA*	L,M	4
Peptidase B (l-leucylglycylglycine) (3.4.11.-)	PEPB*	L,M	4
Peptidase 3 (resolved with both substrates)	PEP-3*	L,M	4
Superoxide dismutase (1.15.1.1)	sSOD*	L	3
Xanthine dehydrogenase (1.1.1.204)	XDH*	L	1,3

[a] Tissues: L, liver; M, muscle; E, eye (retina).

[b] Buffers: 1, Tris-citric acid, pH 6.9; 2, Tris-citric acid, pH 8.0; 3, Tris-boric acid EDTA, pH 8.6; 4, lithium hydroxide (recipes adapted from Selander et al. 1971, Shaklee et al. 1982, Waples 1986, and Buth and Murphy 1990).

mon allele (assigned a value of 100) of 20 *M. dentatus* sampled from the Gulf of California, Mexico. Other alleles were labeled according to the mobility of their products relative to this standard. Multiple loci were numbered, with "1" being the most anodal band in *M. dentatus*. Results were also compared with raw allozyme score data from the Vawter et al. (1980) study of *M. dentatus* and *M. martinicus*.

Analysis of Allozyme Data

BIOSYS-1 vers. 1.7 (Swofford and Selander 1981, 1989) was used to compute measures of genetic variability (heterozygosity and number of polymorphic loci), to test conformance with Hardy-Weinberg equilibrium expectations (with Levene's [1949] correction for small samples), and to calculate Nei's (1972) and modified Rogers' (Rogers 1972, Wright 1978) genetic distances between all pairwise combinations of taxa. This program was also used to construct distance Wagner trees (Farris 1972), using modified Rogers' genetic distances (Wright 1978).

RESULTS

Morphological Variation

The three species of the *Mulloidichthys martinicus* complex share the following fin-ray and lateral-line scale counts: dorsal rays VIII-I,8; anal rays I,8; pectoral rays 15–18 (usually 16 or 17); principal caudal rays 15; and lateral-line scales 35–38 (discounting 3 pored scales on base of caudal fin). There are modally 17 pectoral rays in *M. vanicolensis* and 16 in the other two species (Table 2). Lower-limb gill-raker counts of *M. vanicolensis* are significantly greater than those of *M. martinicus* and *M. dentatus* (Table 3). Those of *M. dentatus* are significantly lower than those of the other two species. There are also some differences in mean lengths of the barbels (Table 4) and pectoral fins (Table 5) between *M. vanicolensis* and the other two species.

TABLE 2

PECTORAL FIN-RAY COUNTS OF SPECIES OF THE *Mulloidichthys martinicus* COMPLEX

SPECIES	NO. OF PECTORAL RAYS				
	15	16	17	18	MEAN
M. martinicus	01	25	09	—	16.2
M. dentatus	—	42	12	—	16.2
M. vanicolensis (Pacific)	—	15	30	—	16.7
M. vanicolensis (Indian)	—	16	23	01	16.6

TABLE 3

GILL-RAKER COUNTS OF THE *Mulloidichthys martinicus* COMPLEX

SPECIES	UPPER-LIMB RAKERS					LOWER-LIMB RAKERS										TOTAL GILL RAKERS												
	07	08	09	10	MEAN	18	19	20	21	22	23	24	25	26	MEAN	25	26	27	28	29	30	31	32	33	34	35	36	MEAN
M. martinicus	01	29	12	—	8.3	—	—	01	04	20	14	03	—	—	22.3	—	—	—	01	05	13	15	07	01	—	—	—	30.6
M. dentatus	05	37	12	—	8.1	02	08	19	18	06	01	—	—	—	20.1	01	02	09	16	14	08	04	—	—	—	—	—	28.5
M. vanicolensis (Pacific)	—	11	36	13	9.0	—	—	—	—	—	07	26	20	07	24.5	—	—	—	—	—	—	01	11	20	10	06	02	32.0
M. vanicolensis (Indian)	01	09	12	01	8.6	—	—	—	—	06	10	06	01	—	23.1	—	—	—	—	03	04	02	08	03	03	—	—	31.6

ANOVA lower-limb raker differences between species: $F = 221.08$; $P < 0.0001$; df $= 2$, 176. ANOVA lower-limb raker differences between Pacific and Indian Ocean populations of *M. vanicolensis*: $F = 42.64$; $P < 0.0001$; df $= 1$, 81.

TABLE 4

BARBEL LENGTH OF THE *Mulloidichthys martinicus* COMPLEX, EXPRESSED AS A PERCENTAGE OF THE STANDARD LENGTH (SL)

SPECIES	NO. OF SPECIMENS	RANGE IN SL (mm)	RANGE IN BARBEL LENGTH (mm)	MEAN BARBEL LENGTH (mm)
M. martinicus	23	112–275	18.9–23.9	20.9
M. dentatus	22	114–270	17.6–24.5	20.4
M. vanicolensis (Pacific)	24	122–262	20.0–26.0	22.9
M. vanicolensis (Indian)	22	114–243	19.2–25.0	22.3

TABLE 5

PECTORAL-FIN LENGTH OF THE *Mulloidichthys martinicus* COMPLEX, EXPRESSED AS A PERCENTAGE OF THE STANDARD LENGTH (SL)

SPECIES	NO. OF SPECIMENS	RANGE IN SL (mm)	RANGE IN PECTORAL LENGTH (mm)	MEAN PECTORAL LENGTH (mm)
M. martinicus	23	119–275	18.0–21.8	19.7
M. dentatus	24	114–270	17.9–21.5	20.1
M. vanicolensis (Pacific)	20	122–262	19.2–23.2	21.1
M. vanicolensis (Indian)	22	114–243	19.2–22.8	20.8

Gill-raker counts of *M. vanicolensis* from the Pacific are significantly different from those from the western Indian Ocean (Sri Lanka to East Africa) (Table 3), although the difference is not as great as that between *M. dentatus* and *M. vanicolensis* from the Pacific. There is also a difference in life color between populations in the western Indian Ocean and the Pacific Ocean. In the Indian Ocean fish, the narrow blue stripes marginal to the mid-lateral yellow stripe are more distinct (Plate I). J.E.R. has observed *M. vanicolensis* in Kenya to school with the blue-striped snapper, *Lutjanus kasmira* (Forsskål), much as *M. mimicus* Randall & Guézé schools with *L. kasmira* in the Marquesas and Line islands (Randall and Guézé 1980).

Allozyme Variation

Genotypic data for all variable loci of *M. martinicus* (Gulf of California) and *M. vanicolensis* (Guam, Tahiti, Easter Island, Hawaii, and Indian Ocean populations) are reported in Table 6. Allozymes used in data analyses included those in Table 1, with the exception of *ACP-1* *, which was not resolved in the Guam, Tahiti, and Easter Island populations (see Table 6). Measures of genetic variability are given in Table 7. All populations conformed to Hardy-Weinberg equilibria, insofar as that can be determined from limited samples.

Both species sampled (*M. dentatus* and *M. vanicolensis*) have 15 polymorphic loci (of 42). Mean heterozygosity per locus of *M. vanicolensis* (summed for all populations) is 0.63, which is less than that of *M. dentatus* (Table 7). Two allelic differences distinguish *M. vanicolensis* from *M. dentatus*: the fixed *b* allele of *PGDH* * in the former and *a* in the latter, and the *d* allele of *XDH* * of *M. vanicolensis* (Table 6). In addition, the *b* allele of *mAAT* * is fixed in *M. vanicolensis*.

Populations of *M. vanicolensis* appear to show close genetic relationship (Tables 6 and 7, Figure 2). Populations from Tahiti and Guam cluster together, sharing the *b* allele at the *sAAT-1* * locus (also shared with *M. dentatus*). This group showed closest relationship to the population from Easter Island.

TABLE 6

Genotypic Distributions of Variable Loci for Goatfish Populations

		NO. OF EACH GENOTYPE PER SPECIES AND POPULATION					
		1 M. d.[b]	2	3	4 M. v.	5 M. v.	6 M. v.
LOCUS	MIGRATION DISTANCE[a]	GULF OF CALIFORNIA	M. v.[b] GUAM	M. v. TAHITI	EASTER ISLAND	HAWAIIAN ISLANDS	INDIAN OCEAN
ACP-1*	*a: 100	aa: 04	XXX[c]	XXX	XXX	aa: 11	aa: 02
	*b: 130						ab: 03
sAH-A1*	*a: 100	aa: 16	aa: 01	ab: 01	ab: 02	aa: 12	aa: 02
	*b: 070	ab: 03	ab: 01				ab: 03
	*c: 095	ac: 01					
ADH-A*	*a: 100	aa: 16	aa: 02	aa: 01	aa: 02	aa: 12	aa: 05
	*b: 115	ab: 04					
ADH-B2*	*a: 100	aa: 18	aa: 01	aa: 01	aa: 02	aa: 12	aa: 05
	*b: 175	ab: 02	ab: 01				
sAAT-B1*	*a: 100	aa: 07	aa: 01	ab: 01	aa: 01	aa: 12	aa: 05
	*b: 120	ab: 12	ab: 01		ab: 01		
		bb: 01					
sAAT-A2*	*a: 100	aa: 19	aa: 01	aa: 01	aa: 02	aa: 12	aa: 05
	*b: 105	ab: 01	ab: 01				
mAAT-A3*	*a: 100	aa: 18	bb: 02	bb: 01	bb: 02	bb: 12	bb: 05
	*b: 070	ab: 02					
FH-A*	*a: 100	aa: 20	aa: 02	aa: 01	aa: 02	aa: 10	aa: 03
	*b: 130					ab: 02	ab: 02
G6PDH-2*	*a: 100	aa: 15	aa: 02	aa: 01	aa: 02	aa: 12	aa: 05
	*b: 120	ab: 02					
	*c: 140	ac: 03					
GPI-A1*	*a: 100	aa: 20	aa: 02	aa: 01	aa: 02	aa: 07	aa: 01
	*b: 110					ab: 03	ac: 02
	*c: 120						cc: 02
G3PDH-A2*	*a: 100	aa: 20	aa: 02	aa: 01	aa: 02	aa: 12	ab: 03
	*b: 150						ac: 02
IDDH-A*	*a: 100	aa: 19	aa: 02	aa: 01	aa: 01	aa: 09	aa: 01
	*b: 110	ab: 01				ac: 03	ad: 02
	*c: 130						dd: 02
	*d: 120						
sIDHP-A1*	*a: 100	aa: 20	ab: 02	aa: 01	ab: 02	aa: 12	aa: 03
	*b: 120						ab: 02
LDH-A2*	*a: 100	aa: 14	aa: 02	aa: 01	aa: 02	aa: 12	aa: 03
	*b: 065	ab: 06					ac: 02
	*b: 120						
sMDH-A2*	*a: 100	aa: 15	aa: 02	aa: 01	aa: 02	aa: 10	aa: 02
	*b: 130	aa: 14	aa: 02	aa: 01	aa: 02	aa: 10	aa: 05
	*b: 120	ab: 06				ac: 02	
	*c: 080						
PGDH-A*	*a: 100	aa: 20	bb: 02	bb: 01	bb: 02	bb: 12	bb: 05
	*b: 115						
PEP-3*	*a: 100	aa: 05	aa: 01	ab: 01	ab: 02	aa: 09	aa: 05
	*b: 125	ab: 12	ab: 01			ab: 03	
		bb: 03					
SOD-A*	*a: 100	aa: 04	aa: 02	aa: 01	aa: 02	aa: 12	aa: 05
	*b: 250	ab: 03					
XDH-A*	*a: 100	aa: 10	dd: 02	dd: 01	dd: 02	dd: 10	dd: 05
	*b: 110	ab: 06				ad: 02	
	*c: 095	ac: 02					
	*d: 080						

[a] Migration distance is relative to the most common allele (designated "a" and assigned a value of 100% of the Gulf of California population of M. dentatus; see Materials and Methods).

[b] M. d. = Mulloidichthys dentatus; M. v. = Mulloidichthys vanicolensis.

[c] XXX, locus not resolved for this population.

TABLE 7

HETEROZYGOSITY AND POLYMORPHISM VALUES

SPECIES	POPULATION (SAMPLE SIZE)	MEAN H PER LOCUS	MEAN NO. OF ALLELES PER LOCUS	% POLYMORPHISM
M. dentatus				
	Gulf of California (20)	0.10 ± 0.03	1.46 ± 0.10	38.46
M. vanicolensis				
	Guam (2)	0.09 ± 0.04	1.15 ± 0.06	15.38
	Tahiti (1)	0.08 ± 0.04	1.08 ± 0.04	07.69
	Easter Island (1)	0.08 ± 0.04	1.08 ± 0.04	07.69
	Hawaii (12)	0.04 ± 0.01	1.21 ± 0.07	20.51
	Indian Ocean (5)	0.11 ± 0.04	1.23 ± 0.08	20.51

GENETIC DISTANCE FROM ROOT
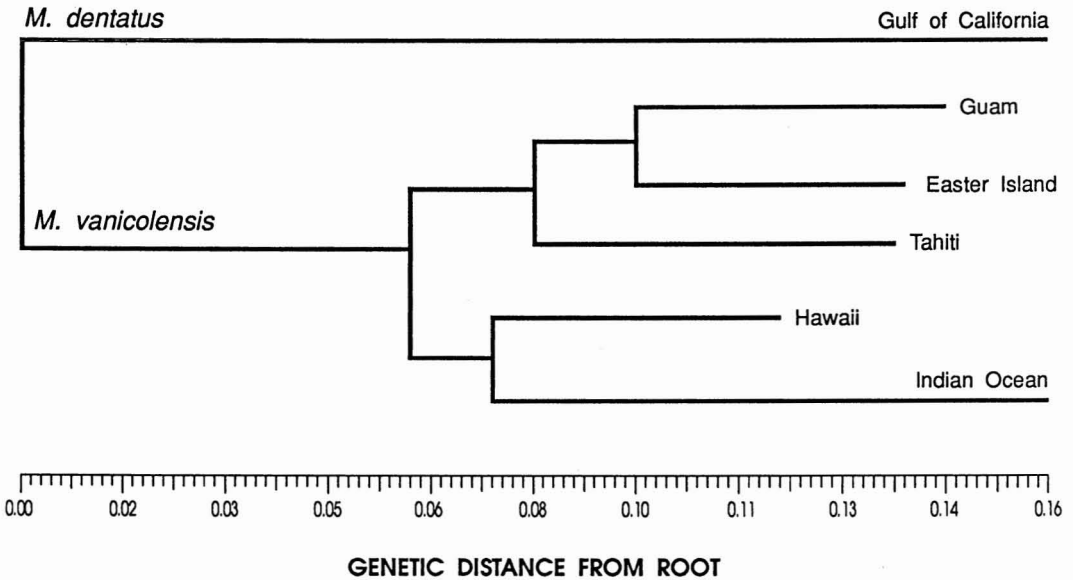
FIGURE 2. Distance Wagner tree, calculated from modified Rogers' genetic distances (Wright 1978, table 8), illustrating relationships among *Mulloidichthys* species and populations and showing relative genetic distances (add lengths of horizontal branches for genetic distances among taxa), rooted to the Gulf of California population of *M. dentatus*. Total length of tree = 0.55. Cophenetic correlation of tree = 0.99.

The population from the Indian Ocean is closest in genetic distance to that from the Hawaiian Islands (Figure 2). The Hawaiian Island population is characterized by an apparently unique *b allele at the *GPI-A** locus and the loss of the *b allele at the *sAH-1** locus. With the Indian Ocean population and *M. dentatus*, it shares *b alleles at the *sMDH-A** and *FH** loci. It would be of interest to obtain comparable data from other areas such as the Indo-Malayan region and southern Japan.

The Indian Ocean population is characterized by three apparently unique alleles (all heterozygous loci with more common alleles shared with the other populations): *c at the *GPI-A** locus, *d at *sIDHP**, and *c at *LDH-A**.

DISCUSSION

Genetic Differences among Species

A comparison of allozyme score data from Vawter et al. (1980) with those from our study (Table 6) indicates that *M. martinicus* is distinguished from both *M. vanicolensis* and *M. dentatus* by the following fixed alleles: a slow allele for *EST-2**, a fast allele for *G6PDH-1**, and a fast allele for *GDH**. The Vawter et al. (1980) data also show a unique slow allele at the polymorphic *EST-1** locus in *M. martinicus*. Alleles that are predominant and have identical migration distances (designated **a* or "100"; see Table 6) in all three species are found at the following loci: *ADH-1**, *ADH-2**, *EST-1**, *G6PDH-2**, *GPI-1**, *LDH-A**, *sMDH-A**, *sMDH-1**, *MPI**, *PEP-A**, and *PGM-1**.

Results of our study indicate that the species *M. vanicolensis* and *M. dentatus* are genetically separable by three apparent allozyme differences (see *Results*). Nei's (1972) genetic distances among *M. dentatus*, *M. martinicus*, and *M. vanicolensis* correspond to distance levels separating closely related species, as characterized by Thorpe (1983), who examined 900 congeneric species comparisons. Vawter et al. (1980) reported a Nei's (1972) genetic distance of 0.168 between *M. martinicus* and *M. dentatus*, which is greater than that estimated between the latter and *M. vanicolensis* in our study (0.087 to 0.115) and indicates greater genetic divergence among the former taxa. This difference appears significant because a greater number of loci and specimens were surveyed in our study (42 loci in this study versus 23 loci and 9 specimens of *M. martinicus* and 17 *M. dentatus* by Vawter et al. [1980]).

Shaklee et al. (1982) electrophoretically analyzed nine species of Hawaiian goatfishes, including *M. vanicolensis*. They found a large Nei's (1972) genetic distance of 0.34 between *M. vanicolensis* and *M. flavolineatus* (Lacépède), which are readily distinguishable by body shape, snout length, number of gill rakers, and coloration differences (Randall et al. 1990). The genetic distance (0.11) separating the two species of goatfish most similar in

morphology [*Parupeneus bifasciatus* (Lacépède) and *P. chryserydros* (Lacépède) = *cyclostomus*] in the Shaklee et al. (1982) study is similiar to that separating *M. vanicolensis* and *M. dentatus* in our study. The two sympatric *Parupeneus*, however, are readily separable on the basis of morphology in contrast to the allopatric members of the *martinicus* complex.

Rosenblatt and Waples (1986) compared allopatric populations of 11 trans-Pacific shore fish species. Three of these are circumtropical, and they were able to compare the Caribbean population of *Priacanthus* (= *Heteropriacanthus*) *cruentatus* (Lacépède) and *Diodon holocanthus* Linnaeus with those of the Pacific. Nei's (1972) genetic distances between the Pacific populations ranged from <0.01 to 0.06, with Atlantic and Pacific populations separated by distances of 0.19 (*D. holocanthus*) and 0.14 (*H. cruentatus*). They attributed the low level of differentiation within the Pacific either to recent immigration or, more likely, to gene flow across the East Pacific Barrier. The trans-Pacific populations of these species showed little morphological or genetic divergence, in contrast to the species of *Mulloidichthys*, which are distinguishable both morphologically and genetically.

Population Relationships of M. vanicolensis

Mean heterozygosity levels (direct count) for populations of *M. vanicolensis* (Table 7) approximate previous estimates from allozyme data for other marine fishes (Winans 1980, Kirpichnikov 1981, Beckwitt 1983, Waples and Rosenblatt 1987, Stepien and Rosenblatt 1991), including goatfishes (Shaklee et al. 1982). Heterozygosity and percentage polymorphism levels (Table 7) are somewhat higher in *M. dentatus* than in populations of *M. vanicolensis*, which is probably the result of larger sample size in the case of percentage polymorphism (because the overall number of polymorphic loci for all populations sampled is the same in both species), but in the case of heterozygosity the difference appears to be real (because average

heterozygosity for all individuals sampled is lower; see *Results*).

The Hawaiian Island population of *M. vanicolensis* has a lower heterozygosity level than the other populations, despite a much larger sample size. The Hawaiian Archipelago is separated (except for Johnston Island, which has primarily an impoverished Hawaiian fish fauna) from the rest of Polynesia by a deep water gap of ca. 1500 km (Briggs 1974) and has a high rate of shore fish endemism (estimated as ca. 34% by Gosline and Brock [1960] and as 25.0% by Randall [in press]). Low heterozygosity of the Hawaiian population may suggest a genetic bottleneck, either by an original colonization by a few individuals (founder effect) or a reduction in population in the relatively recent past (Holgate 1966, Nei et al. 1975, Chakraborty and Nei 1977). Alternatively, low heterozygosity may be a result of selection eliminating rare alleles.

Genetic distances and Wagner clustering relationships (Figure 2) show slight genetic divergence among populations of *M. vanicolensis*, at levels characteristic of population differences among marine fishes having relatively high estimated dispersal capability and thus little apparent geographic isolation (Rosenblatt and Waples 1986, Stepien and Rosenblatt 1991). In our study, populations of *M. vanicolensis* showed little genetic isolation (D values ranging from 0.01 to 0.04), similar to results obtained for allozyme data from 12 trans-Pacific tropical shore fish pairs (D values ranging from <0.01 to 0.06) examined by Waples and Rosenblatt (1987). In contrast to our study, Nei's (1972) D values between conspecific populations separated by the Isthmus of Panama were markedly higher, ranging between 0.13 and 0.36 (Vawter et al. 1980).

The genetic similarity among populations of *M. vanicolensis* suggests no major barrier to gene flow, which is supported by present geography and ocean current patterns. Easter Island (27° 6′ S, 109° 17′ W) is the most geographically isolated island of the entire Indo-Pacific region. Only 165 species of fishes are known from the island, of which 107 are shore fishes (Randall and Cea Egaña 1984, Di Salvo et al. 1988) and 32% of these are endemic (Randall, in press). In our study, the Easter Island population appears genetically closer to that from Guam than to that from Tahiti, which may well be an artifact of small sample size and is due to greater frequency of the *b allele at the *sAAT-B** locus in the Tahitian sample. There are several species of shore fishes from Easter Island that are found elsewhere only in the Hawaiian Islands (Springer 1982), and a closer relationship to the Hawaiian Island population, as well as to that of Tahiti, was originally expected.

The population of *M. vanicolensis* from the Hawaiian Islands shows some genetic isolation from the other Pacific populations (Figure 2), supported by presence of three unique alleles (Table 6). Its heterozygosity and polymorphism values (Table 7) are also significantly less, suggesting a possible founder effect and/or selection.

It is odd that the population from Oman in the northwestern Indian Ocean appears most closely related to that from the Hawaiian Islands. This is largely due to a shared *b allele at the *FH** locus. They also share a *b allele at the *sMDH-A** locus, which is also present in *M. dentatus*. Apparent absence of these alleles in the populations of *M. vanicolensis* from Guam, Tahiti, and Easter Island may be an artifact of small sample size.

A number of wide-ranging Indo-Pacific reef fishes have slight differences in morphology and/or color between the western Indian Ocean and the western Pacific. Currently, there appears to be no obvious biogeographic barrier to dispersal of shore fishes with pelagic larvae between these regions, although distribution patterns suggest that such a barrier probably once existed (Springer 1982). Woodland (1983, 1986) discussed the probability of an Indo-Malayan region east-west barrier to the distribution of marine fishes during the "Ice Ages."

Opinions vary as to what level of divergence should be recognized as specific. For example, Schultz (1986) recognized two species of turkeyfishes, *Pterois miles* (Bennett) in the Indian Ocean and *P. volitans* Linnaeus in the Pacific Ocean. Randall and Smith (1982), however, preferred not to give nomenclatural recogni-

tion to the Indian Ocean–Pacific variants of the wrasses *Halichoeres hortulanus* (Lacépède) and *H. zeylonicus* (Bennett).

On the basis of the gill-raker counts and color differences between the Indian Ocean and Pacific Ocean populations of *M. vanicolensis*, it might be argued that they are distinct species. However, no fixed differences in allozymes were found, in marked contrast to populations separated by the East Pacific Barrier (*M. vanicolensis* and *M. dentatus*), and, in the absence of other morphological differences, we believe that the most conservative course is to consider the two populations to be conspecific. That gene flow is, however, restricted is indicated by the finding of three unique alleles in a sample of five from the Indian Ocean (versus a sample of 16 from the central and western Pacific). Absence of fixed differences may reflect either gene flow or recency of separation. Gene flow among populations of *M. vanicolensis* may be maintained by a protracted oceanic juvenile stage, as is characteristic of many mullids (Schmidt 1986).

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