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DISPERSAL AND EVOLUTION OF THE PACIFIC BASIN GEKKONID LIZARDS *GEHYRA OCEANICA* AND *GEHYRA MUTILATA*

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Abstract.—The Pacific island geckos *Gehyra mutilata* and *Gehyra oceanica* were studied on several Pacific Basin archipelagos to determine the degree that their distributions have been modified by humans (as commensals), through the analysis of protein variation using starch gel electrophoresis. *Gehyra mutilata* is an anthropophilic species that is widespread in the Pacific Basin and Southeast Asia. No protein variation was found in the Pacific Basin and southern Asia, although there were fixed allelic differences between populations of southern Asia and those further north. These results suggest possible recent human-aided transport across the Pacific from a population that experienced a genetic bottleneck in southern Asia. *Gehyra oceanica*, based on protein variation, consists of two natural groups in the Pacific, a northern (Micronesian) form and a southern (Melanesian and Polynesian) form. The northern form has very similar gene frequencies across its range in Micronesia. The southern form has its greatest allelic diversity in the south-central Pacific. *F*-statistics for *G. oceanica* in the south fall within the range of values in the literature for mainland Australian species of *Gehyra* that are not human commensals and for other island lizards that have been considered as natural dispersers. These values are consistent with the hypothesis that *G. oceanica* was naturally dispersed across the Pacific, prior to the arrival of humans and that the equatorial currents are a barrier to natural, north-south gene flow/dispersal in Pacific Basin lizards. However, human-aided dispersal within the northern and southern regions cannot be ruled out. By comparing the ecology of these two species, *G. oceanica* has the adaptations necessary for natural oversea dispersal, whereas *G. mutilata* has an ecology consistent with human-mediated dispersal, in support of the conclusions from the genetic data.

Key words.—Allozymes, biogeography, dispersal, *F*-statistics, *Gehyra*, gekkonidae, gene flow, Pacific Basin.

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Long-distance insular dispersal has been of interest to biogeographers for a long time (Wallace 1881; Mayr 1953; Darlington 1957). Lizards, birds, and bats are the terrestrial vertebrate groups that have been most successful at long-distance dispersal, and have thus been the subject of much discussion (Simpson 1952; Mayr 1953; MacArthur and Wilson 1967; Adler 1992). Most birds and bats have the ability to fly; therefore, their long-distance dispersal is both expected, and functionally different from that of lizards. However, it is not obvious what behavioral attributes of lizards make them so adept at reaching the far corners of the globe.

There are two basic ways that species of lizards can disperse across ocean barriers to isolated islands (Mayr 1953). The first is naturally by rafting on vegetative mats or floating on the water surface (Wallace 1881; McCann 1953; Brown and Alcala 1957; Darlington 1957; Kluge 1969; Schoener and Schoener 1984), especially at high glacial periods when the sea level is lower and thus the distances between islands are reduced (Gibbons and Clunie 1986; Zug 1991). The second is human mediated as inadvertent commensals in canoes and other oceanic vessels (Loveridge 1945; McCann 1953; Brown and Alcala 1957; Darlington 1957; Kluge 1969; Zweifel 1979). Distributional data for lizards has been used to distinguish these two different dispersal modes. Species that are endemic to single islands or archipelagos are generally considered natural dispersers, whereas species that are widespread across oceanic islands are considered human commensals. In the Atlantic and Indian Ocean islands, natural dispersal is generally accepted as the primary mode of transport for lizards between islands, except for some recent invaders, because most species are endemic to single island groups (Kluge 1969; Vinson and Vinson 1969; Blanc 1973; Klemmer 1976; Cheke 1984). However, in the Pacific Ocean, human-mediated dispersal has been invoked as the main mode of transport for lizards to many islands (Loveridge 1945; Darlington 1957; Zweifel 1979; King and Horner 1989; Zug 1991; Beckon 1992). The primary reason for this difference between oceans is the long history of human habitation in the Pacific (Bellwood 1979), combined with presumed morphological uniformity of widespread lizard species across the Pacific. This pattern has been interpreted as representing genetic uniformity resulting from recent human-aided dispersal (Burt and Burt 1932; Kluge 1969; Zweifel 1979; King and Horner 1989).

The Pacific Basin has experienced three different waves of human movements, each having a different source (Fig 1; Bellwood 1991). The first was of Australoid people who spread from New Guinea to New Britain and the Solomons (northwestern Melanesia) approximately 30,000 years before present, apparently by walking across the low sea level land bridges and crossing the shorter oceanic distances. Beginning about 4000 years before present these people had the maritime technology to disperse the greater oceanic distances to southeastern Melanesia (Vanuatu, Fiji, New Caledonia, Tonga, Samoa) and Western Micronesia (Fig. 1; Hagelberg and Clegg 1993). The next major movement was of a different people, the proto-Polynesians, coming from southern Asia, beginning 3000 years before present. They bypassed most of Melanesia on their route to the uninhabited eastern Pacific (Fig. 1; the "express train to Polynesia" model, Diamond 1988; Hagelberg and Clegg 1993). The third major invasion by humans began 300 years ago and has continued through the present as Europeans explored and transported goods

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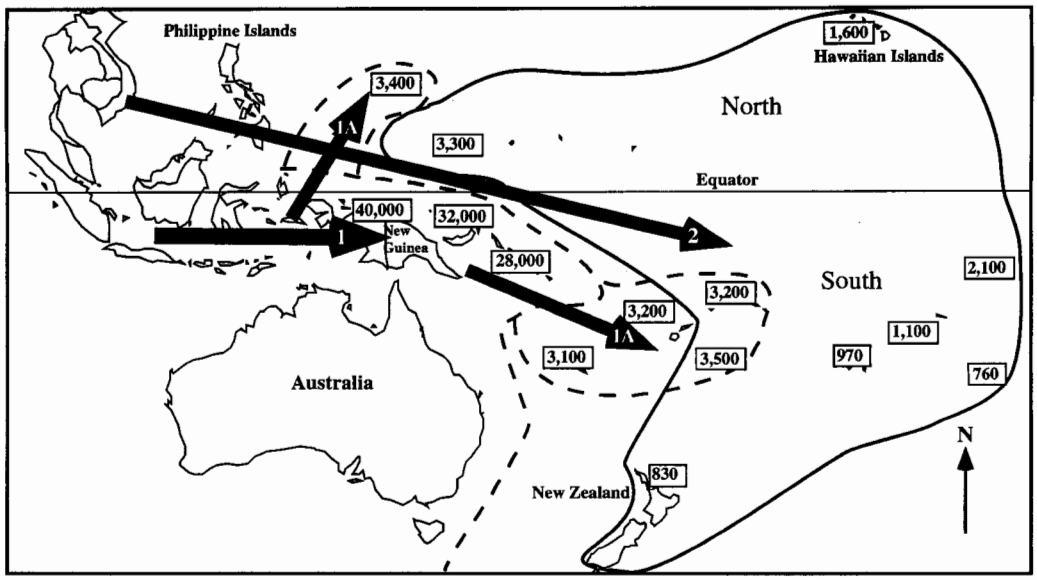

FIG. 1. Dispersal routes used by humans during the different colonizations of the Pacific (based on mtDNA data of Hagelberg and Clegg 1993). Dates (years before present) of first human arrival to several island groups shown in boxes (Nunn 1990). The western Melanesian islands, bounded to the east by the dashed line, were invaded by Australoid people (arrow 1) followed by those islands enclosed by dashed lines (arrows 1A), both during the first colonization. The islands outlined by the solid line were colonized by the proto-Polynesians, from southern Asia, during the second invasion (arrow 2). All islands have been exposed to Europeans during the recent (third) colonization of the Pacific.

across the Pacific Basin. All three of these movements have been implicated in the dispersal of various plants and animals across the Pacific, with the last two movements being the most significant and widespread (Kirch and Yen 1982; Flannery et al. 1988; Lebot et al. 1991; Roberts 1991; Case et al. 1994).

To distinguish the degree to which human-mediated transport and natural dispersal are alternative modes of invasion and dispersal for Pacific Ocean lizards, explicit hypotheses must be addressed with molecular techniques (when archeological data is lacking), through the following steps. The first step is to determine what the predicted genetic pattern would be for the human-aided transport hypothesis, based on historic and recent human movement patterns. The second step is to determine what the predicted genetic pattern would be for a naturally dispersed species based on natural phenomena, such as oceanic currents and cyclones. Third, if the human- and natural-predicted genetic patterns do not differ, then they cannot be distinguished, but if they do, then we may be able to reject one or the other. Last, compare the genetic pattern found in the study species to these two hypothetical patterns. A good match to one but not the other pattern would support primarily one of these hypotheses; an intermediate fit would indicate that natural dispersal is being augmented with human transport. Archaeological studies could support natural dispersal if a species were recorded in fossil layers prior to cultural artifacts. These studies of the Pacific are rare and only recently findings have disproven the human dispersal hypothesis for a few species in Tonga in the Pacific (Pregill 1993).

There are two widespread families of lizards in the Pacific, the Scincidae and the Gekkonidae. For this study, I focus on the family Gekkonidae and the genus *Gehyra* to test these hypotheses. Many species of geckos are human commensals, and therefore their dispersal might be consistent with human transport (Kluge 1969; Zug 1991; Case et al. 1994). The genus *Gehyra* is the only gekkonid genus in the Pacific with widespread sympatric sexual species. These are *Gehyra oceanica* and *Gehyra mutilata*, which coexist on many islands. *Gehyra oceanica* is widespread throughout the Pacific basin and is apparently restricted to this region. The single analysis of karyotypic variation of this species found that populations across the southern and eastern Pacific were invariant; these results were interpreted as resulting from human-mediated transport (King and Horner 1989). The analysis of the morphology of these same populations and several others indicated relatively little between-population variability, further supporting the conclusion of their karyotype study (King and Horner 1989). A more recent analysis of morphological character variation also concluded that *G. oceanica* was transported by humans historically, although differences in preanal-femoral pore counts were found between the northern and southern regions of the Pacific (Beckon 1992). Beckon (1992) suggested that this pattern correlates with the distribution of human races, Micronesia versus Melanesia and Polynesia, through the historical transport by humans and the inability of these geckos to maintain gene flow between islands once they had invaded. This resulted in a pattern of morphological differences that correlates with the distribution of different recognized human races in the Pacific. Recent mtDNA data for humans are changing the historic view of human races in the Pacific (Fig. 1; Hagelberg and Clegg 1993). Zug (1991) was the first to suggest that *G. oceanica* may be a naturally dispersed species and that it was able to invade the Pacific during the early to mid-Miocene.

Gehyra mutilata is widespread throughout the Pacific Ba-

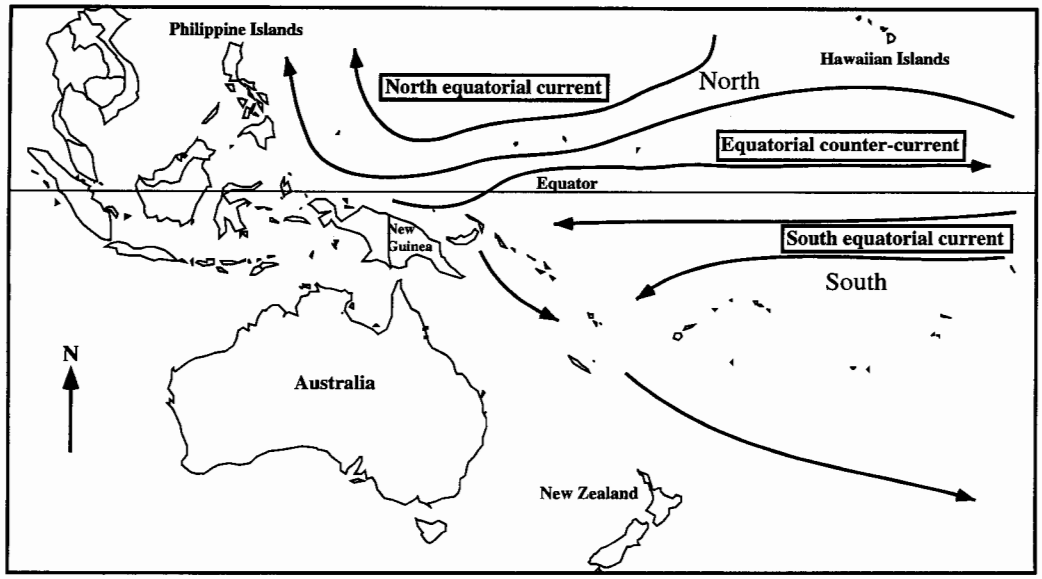

FIG. 2. Major currents across the tropical Pacific (modified from Nunn 1994). Notice that none traverse either north to south or vice versa across the equator.

sin, large regions of Southeast Asia, and the Indian Ocean. It is the least studied, widespread gecko in the world. Its karyotype is still unpublished (Ota pers. comm.), and no studies have been completed of its population genetics or morphological variation across its distribution. These two species differ in body size by half (*G. oceanica* is the larger species), and therefore they may have different dispersal capabilities (Zug 1991). These congeneric species may evolve at similar rates due to similar life-history parameters, although their generation times probably differ as a result of the size difference.

MATERIALS AND METHODS

Hypotheses

Step 1.—The human-aided transport hypothesis predicts a genetic pattern of southwest to east disjunction in the Pacific, if the particular species was transported by humans prior to the arrival of Europeans. The archipelagos of the Marianas, Solomons, Vanuatu, and Fiji should be more similar to each other than to the archipelagos to the east, because they were colonized earlier by humans from New Guinea as the source (Fig. 1). In contrast, those populations to the east were colonized more recently, and by humans from southern Asia as a source. This difference might be reflected through allelic frequency differences, or allelic fixation, representing different genetic histories for the two sets of populations. A species transported with Europeans recently might show no discrete genetic pattern with respect to geography if it did not experience strong genetic bottlenecks, or had multiple origins into the Pacific (Moritz et al. 1993). Alternatively, a species could be genetically similar across all of its Pacific populations. This could indicate a recent genetic bottleneck stemming from the introduction of only a few individuals from a single source.

Step 2.—The natural dispersal hypothesis predicts a north to south disjunction in the Pacific. This would result from dispersal in the east to west parallel currents both north and south of the equator. However, since no currents travel north to south or vice versa (Fig. 2), gene flow would be restricted across the equator. The pattern of annual tropical cyclones precludes gene flow across the equator also, as cyclones travel outside of the region 5°N to 5°S of the equator (Nunn 1994). If a species had a long history in the Pacific, then some genetic subdivision should be expected even if it did experience a genetic bottleneck when it initially colonized the region, as it may have had enough time to reestablish genetic variation through mutation.

Therefore the alternative hypotheses are: (1) human-mediated transport: non-European (southwest to east disjunction in the Pacific Basin), and European (no discrete genetic pattern with respect to geography, or widespread genetic similarity across all populations); (2) natural dispersal (north to south disjunction in the Pacific Basin).

Step 3.—The hypotheses differ substantially in their geographic predictions of genetic patterns; therefore they have the potential to be discriminated with genetic data for a species from across the Pacific.

Step 4.—This step involves collecting the following genetic data, and comparing the results to these alternative hypotheses.

Natural History of Gehyra oceanica and Gehyra mutilata

Both gecko species occur widely across the Pacific Basin, with *G. oceanica* being confined to this region. *Gehyra oceanica* was historically thought to occur on New Guinea, and in Australia, but King and Horner (1989) have shown these populations to be other species. *Gehyra mutilata* occurs also in southeast Asia, across the Indian Ocean islands, and in Mexico. Both species may occur in natural forests, disturbed garden areas, or urban areas, and they are both arboreal and

TABLE 1. *Gehyra oceanica* collection data. Voucher specimens are deposited at the California Academy of Sciences, United States National Museum, and the Australian Museum.

Localities	Map #	Abbreviation	Collection date	Sample size
Solomon Islands				
Guadalcanal, Choisel	1	SOLO	Nov. 1988	6
Vanuatu				
Efate	2	VAEF	Dec. 1988, Feb. 1993	32
Emao	3	VAEM	Dec. 1988	14
Fiji				
total of six islands	4	FIJI	1988, 1989, 1991, 1992, 1993	43
Beqa	5	BEQA	Feb., Mar. 1993	33
Tonga				
Tongatapu, Eua	6	TONG	Zug and Ineich 1992	23
Western Samoa				
Upolu	7	WSUP	Nov. 1988; Aug., Sept. 1990; 1992	22
Savai'i	8	WSSA	Nov. 1988; Aug., Sept. 1990; 1992	21
Cook Islands				
Atiu, Rarotonga	9	COOK	Sept. 1989, Sept. 1991	14
Society Islands				
Moorea, Tahiti	10	SOCI	Oct. 1989	12
Tuamotu Archipelago				
Takapoto, Rangiroa	11	TUAM	Oct. 1989; Feb., Mar. 1993	13
Marquesas Islands				
Nuku Hiva, Ua Pu	12	MARQ	Oct. 1989	9
Marshall Islands				
Arno Atoll	13	MARS	Dec. 1991, Jan., Feb. 1993	22
Caroline Islands				
Kosrae	14	KOSR	Dec. 1991	6
Pohnpei	15	POHN	Dec. 1991	9
Mariana Islands				
Rota	16	ROTA	June, Sept. 1990	6

typically nocturnal. *Gehyra oceanica* obtains a maximum snout vent length (SVL) of 102 mm (Beckon 1992), and *G. mutilata* an SVL of 50 mm (Zug 1991). Both species lay two eggs, although they differ in that *G. mutilata* eggs are adherent to each other and the substrate, compared to *G. oceanica*, which lays nonadhesive eggs (Zug 1991).

Sampling

Specimens of *G. oceanica* were collected from 27 island populations from 12 archipelagos across the Pacific representing the majority of island groups where it occurs (Table 1; Fig. 3). These represented multiple populations of two of

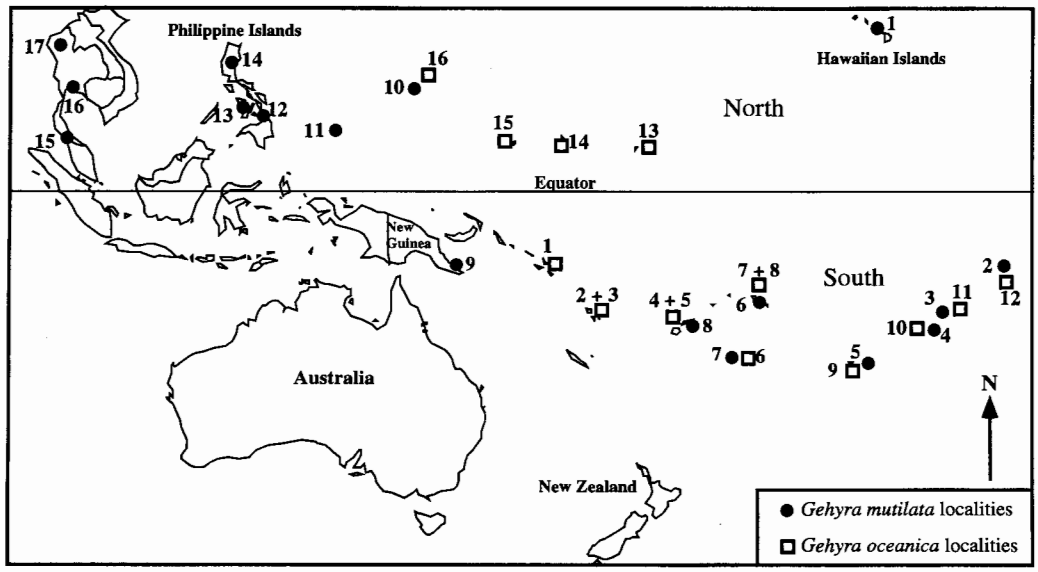

FIG. 3. Sample localities for both species of *Gehyra*.

TABLE 2. *Gehyra mutilata* collection data. Voucher specimens are deposited at the California Academy of Sciences, United States National Museum, and the Texas Memorial Museum.

Localities	Map #	Abbreviation	Collection date	Sample size
Hawai'ian Islands				
Kauai, Maui, Hawai'i	1	HAWA	Sept. 1988, Oct. 1989, Aug. 1990	42
Marquesas Islands				
Nuku Hiva, Ua Pu	2	MARQ	Oct. 1989	7
Tuamotu Archipelago				
Takapoto, Rangiroa	3	TUAM	Oct. 1989	6
Society Islands				
Moorea, Tahiti	4	SOCI	Oct. 1989	3
Cook Islands				
Atiu	5	COOK	Sept., Oct. 1989	9
Western Samoa				
Upolu, Savai'i	6	WSUP	Nov. 1988; Aug., Sept. 1990; 1992	11
Tonga				
Tongatapu, Eua	7	TONG	Zug and Ineich 1992	7
Fiji				
Taveuni	8	FIJI	Oct. 1990	4
Papua New Guinea				
Fergusson	9	PNGF	Dec. 1991	1
Mariana Islands				
Guam, Rota	10	MARI	June, Sept. 1990	12
Belau				
Koror, Babeldoap	11	BELA	Sept. 1990, Dec. 1991	6
Philippine Islands				
Caminguin	12	PICA	Sept. 1990	1
Negros	13	PINE	Sept. 1990	3
Luzon	14	PILU	Sept. 1990	2
Thailand				
Thalebon Park	15	THTH	Oct. 1988	5
Bangkok	16	THBA	Oct. 1988	7
Doi Suthep + Inthanon	17	THDO	Oct. 1988	5

Beckon's (1992) morphotypes, and five of the seven populations that King and Horner (1989) karyotyped. Specimens of *G. mutilata* were collected from 10 oceanic populations representing most of the island groups where they occur, plus one New Guinea, three Philippine, and three Thailand populations (Table 2; Fig. 3). Most of the individuals were found at night on forest and garden trees, and on buildings, or occasionally during the day under bark on trees and in leaves of banana trees.

Electrophoretic Methods

Most specimens were sacrificed within a few days of capture. Tissues (body wall and tail muscle, and liver) were stored either in liquid nitrogen or on dry ice in the field and then transferred to a −80°C freezer. A few specimens of *G. oceanica* were collected as eggs, hatched in the field, and sacrificed. Some specimens died up to two days before access to an ultracold freezer for tissue storage, but there did not appear to be an effect on most proteins scored. A small sample (0.1 to 1.0 grams) of each of the tissues was ground separately with distilled water and then spun at 14,000 rpm for two minutes in a microcentrofuge. The samples were then either used directly for electrophoresis or refrozen at −80°C.

The methods used for horizontal starch-gel electrophoresis follow Rank (1992) and Murphy et al. (1990). Gels varied in their running conditions from three hours to 17 hours. All gels were run in a glass-fronted refrigerator between 50–150 volts and 25–100 milliamps. Staining followed Harris and Hopkinson (1976) and Murphy et al. (1990) for the proteins in Table 3.

Statistical Analysis

Two sets of analyses were completed for the *G. oceanica* dataset to determine the distribution of genetic variation, and what model for dispersal best explains that variation. These were done using BIOSYS-1 (Swofford and Selander 1981), and Weir and Cockerham's (1984) modification of Wright's *F*-statistics (Wright 1978; program by Tim Holtsford). The data for *G. mutilata* were not analyzed statistically (see Results section).

BIOSYS-1 was used to obtain allelic frequencies for estimating heterozygosity, percent polymorphic loci, and Nei's (1978) and Rogers's (1972) genetic distances for the 16 populations in Table 1. Nei's genetic distances were used to obtain a UPGMA cluster diagram to identify if there was a geographic pattern of relationships, which might be consistent with one of the alternative hypotheses. The populations in Table 1 were next combined within archipelagos, to reduce the number of populations to 12, and then subdivided (based on the sample sizes from various sites; all populations had a minimum sample size of six individuals) within some populations to make a total of 20 populations and Nei's (1978) genetic distances were obtained for these two datasets. Then UPGMA cluster diagrams were obtained and these were compared with the initial analysis for differences, that might be due to intraarchipelago variation.

TABLE 3. Loci scored, buffer systems, and tissue analyzed for electrophoresis.

Enzyme system	Enzyme commission number	Locus	Buffer conditions*	Tissue**	Number of loci
Aconitase hydratase	4.2.1.3	ACOH	D	L,M	2
Adenosine deaminase	3.5.4.4	ADA	C	L	1
Adenylate kinase	2.7.4.3	AK	E	M	1
Alcohol dehydrogenase	1.1.1.1	ADH	C	L	2
Aspartate aminotransferase	2.6.1.1	AAT	A,I	L	2
Carbonate dehydratase	4.2.1.1	CA	F	L	1
Creatine kinase	2.7.3.2	CK	B	M	1
Enolase	4.2.1.11	ENO	H	L	1
Fumarate hydratase	4.2.1.2	FUMH	I	L	1
Glucose-phosphate isomerase	5.3.1.9	GPI	E	M	1
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	GAPDH	G	M	1
Glycerol-3-phosphate dehydrogenase	1.1.1.8	G3PDH	D	M	2
Iditol dehydrogenase	1.1.1.14	IDDH	F	L	1
Isocitrate dehydrogenase	1.1.1.42	IDH	D	L	2
Lactate dehydrogenase	1.1.1.27	LDH	F,G	L	2
Malate dehydrogenase	1.1.1.37	MDH	D	M	2
Mannose-phosphate isomerase	5.3.1.8	MPI	D,E	M	2
Peptidase (Leu-ala substrate)	3.4.11.-	PEP-1	A	M	1
Peptidase (Leu-gly-gly substrate)	3.4.11.-	PEP-2	A	M	1
Peptidase (Leu-leu-leu substrate)	3.4.11.-	PEP-3	A	M	1
Peptidase (Phe-pro substrate)	3.4.11.-	PEP-4	A	M	1
6-Phosphogluconate dehydrogenase	1.1.1.44	6-PGD	E	M	1
Phosphoglycerate kinase	2.7.2.3	PGK	G	M	1
Phosphoglucomutase	2.7.5.1	PGM	H	L	2
Superoxide dismutase	1.15.1.1	SOD	I	L	2

* A: Phosphate-citrate (mercap); B: Tris-citrate pH 6.7; C: Tris-citrate pH 6.7 (mercap); D: Tris-citrate pH 8.0; E: Tris-citrate pH 8.0 (NADP); F: Tris-citrate pH 8.0 (mercap); G: Tris-citrate pH 8.0 (mercap and NAD); H: Tris-maleate; I: Poulik pH 8.7.
** M: Muscle; L: Liver.

Levels of differentiation between subpopulations were measured using Weir and Cockerham's (1984) modification of Wright's *F*-statistics (Wright 1978). These were calculated for each population using the genotype frequencies for each locus. I focused my analysis on the estimator F_{ST} (called theta by Weir and Cockerham 1984), which is the genetic subdivision among populations, based on each locus's departure from heterozygosity levels expected for panmictic populations. The values for F_{ST} should be between 0 and 1, with low values indicating high levels of gene flow between populations, and high values of F_{ST} suggesting genetic subdivision between populations. I first calculated F_{ST} for all populations together, then I divided the data into four northern and 12 southern populations and recalculated F_{ST} to see whether there was differentiation across these areas as Beckon (1992) had found for preanal-femoral pore numbers. The standard errors for the *F*-statistics were obtained by jackknifing across loci (Weir and Cockerham 1984; Hellberg 1995). I then did this same analysis for the minimal (12) and maximal (20) population subdivisions used above to determine if there was any impact on the *F*-statistics.

RESULTS

Proteins corresponding to 31 loci could be scored for the majority of populations of *G. oceanica* and 25 loci could be scored for the majority of populations of *G. mutilata*. Of these, *G. oceanica* was polymorphic for 11, although several of these loci had only rare heterozygotes. The subsequent analyses are based on *CK-1*, *G-3-PDH-1*, *IDDH*, *LDH-2*, and *6-PGD*, the five polymorphic loci that I was able to score for all populations of *G. oceanica*. For *G. mutilata* only seven loci were polymorphic and a few others had rare heterozygotes. Only *IDDH*, *MPI-1*, and *6-PGD* were scored for all populations; I was unable to rerun individuals to homologize alleles for several other loci as apparently the homogenate had degraded.

Gehyra oceanica

Genetic Variation.—The genotypic frequencies for the five polymorphic loci scored for all 16 *oceanica* populations are presented in Table 4. Three major patterns are apparent in the allele frequency variation. First, the 12 southern populations average 3.7 polymorphic loci per population, whereas the four northern populations have polymorphism at only two of the five loci, (*IDDH*, and *G-3-PDH-1*). Second, all alleles are present in at least five populations. Third, all alleles present in the northern populations are a subset of those in the south, although allele *d* for *IDDH*, which was in high frequency in the north was only found in the samples from Efate, Vanuatu, and Fiji in the south and at a low frequency. I mapped allele frequencies for the two loci that were polymorphic in the most populations (*IDDH*, and *G-3-PDH-1*), and an obvious north to south division was apparent for both loci (Figs. 4, 5). This division is consistent with the natural-dispersal hypothesis, not the human-aided transport hypothesis.

Table 4 shows the heterozygosity values and the mean number of alleles per locus within populations. The number of alleles per locus varies across islands from 1.2 to 2.8 (Table 4). When the islands are divided into north and south, then the northern islands average 1.35 alleles per locus (SE = 0.05), whereas the southern islands average

TABLE 4. Genotype frequencies for five polymorphic loci for 16 island populations of *Gehyra oceanica*. The bottom has mean sample size per locus (*n*), the mean number of alleles per locus (X), observed heterozygosity (H), and standard error for heterozygosity (SE).

Locus and genotype	Island															
	SOLO	VAEF	VAEM	FIJI	BEQA	TONG	WSUP	WSSA	COOK	SOCI	TUAM	MARQ	MARS	KOSR	POHN	ROTA
CK-1	*4*	*29*	*14*	*39*	*31*	*23*	*22*	*21*	*14*	*12*	*13*	*9*	*22*	*6*	*9*	*6*
aa	1.00	0.86	1.00	0.85	0.61	0.96	0.68	0.81	0.50	0.67	0.84	1.00	1.00	1.00	1.00	1.00
ab	—	0.14	—	0.15	0.29	—	0.23	0.19	0.29	0.33	0.08	—	—	—	—	—
bb	—	—	—	—	0.10	0.04	0.09	—	0.21	—	0.08	—	—	—	—	—
G-3-PDH-1	*6*	*32*	*14*	*41*	*33*	*23*	*22*	*21*	*14*	*12*	*13*	*9*	*22*	*6*	*9*	*6*
aa	1.00	0.81	1.00	0.76	0.97	1.00	0.95	0.81	0.86	1.00	0.46	1.00	—	—	—	—
ab	—	0.09	—	0.12	0.03	—	0.05	0.09	—	—	—	—	—	—	—	—
bb	—	—	—	0.02	—	—	—	—	—	—	—	—	—	—	—	—
ac	—	0.09	—	0.07	—	—	—	0.09	0.14	—	0.54	—	—	—	—	—
bc	—	—	—	—	—	—	—	—	—	—	—	—	0.23	—	0.22	0.33
cc	—	—	—	0.02	—	—	—	—	—	—	—	—	0.77	1.00	0.78	0.67
LDH-2	*6*	*32*	*14*	*43*	*33*	*23*	*22*	*21*	*14*	*12*	*13*	*9*	*22*	*6*	*9*	*6*
aa	0.67	0.34	0.36	0.77	0.76	0.87	0.64	0.67	1.00	0.83	0.62	1.00	1.00	1.00	1.00	1.00
ab	—	0.53	0.57	0.18	0.24	0.13	0.32	0.28	—	0.17	0.23	—	—	—	—	—
bb	0.33	0.13	0.07	0.05	—	—	0.04	0.05	—	—	0.15	—	—	—	—	—
6-PGD-1	*6*	*31*	*14*	*42*	*32*	*23*	*22*	*21*	*12*	*12*	*13*	*9*	*22*	*6*	*9*	*6*
aa	1.00	0.90	1.00	0.98	0.91	0.87	1.00	1.00	0.50	0.67	1.00	0.67	1.00	1.00	1.00	1.00
ab	—	0.03	—	—	0.06	—	—	—	0.17	0.17	—	0.33	—	—	—	—
ac	—	0.06	—	0.02	0.03	0.13	—	—	0.33	0.08	—	—	—	—	—	—
cc	—	—	—	—	—	—	—	—	—	0.08	—	—	—	—	—	—
IDDH-1	*6*	*30*	*13*	*41*	*31*	*18*	*22*	*20*	*11*	*12*	*13*	*8*	*21*	*6*	*9*	*6*
aa	—	0.03	0.08	0.15	0.19	0.44	0.14	0.50	0.45	0.58	0.31	0.63	—	—	—	—
ab	—	0.27	0.38	0.46	0.55	0.56	0.41	0.20	0.45	0.33	0.38	0.38	—	—	—	—
bb	1.00	0.47	0.46	0.29	0.23	—	0.41	0.25	0.10	0.08	0.08	—	0.38	0.33	0.33	0.17
ac	—	0.07	—	0.02	0.03	—	0.04	0.05	—	—	0.23	—	—	—	—	—
bc	—	0.07	0.08	0.05	—	—	—	—	—	—	—	—	—	—	—	—
bd	—	0.07	—	—	—	—	—	—	—	—	—	—	0.19	0.33	0.44	0.33
dd	—	0.03	—	0.02	—	—	—	—	—	—	—	—	0.43	0.33	0.22	0.50
n	5.6	30.8	13.8	41.2	32.0	22.0	22.0	20.8	13.0	12.0	13.0	8.8	21.8	6.0	9.0	6.0
X alleles/locus	1.2	2.8	1.6	2.6	2.4	1.8	2.0	2.2	2.0	2.0	2.0	1.4	1.4	1.2	1.4	1.4
H observed	0.000	0.284	0.207	0.219	0.247	0.163	0.209	0.183	0.277	0.217	0.292	0.142	0.084	0.067	0.133	0.133
(SE)	0.000	0.089	0.128	0.085	0.096	0.102	0.085	0.049	0.094	0.062	0.123	0.087	0.051	0.067	0.089	0.082

2.00 alleles per locus (SE = 0.14). These sets of populations are significantly different (*t*-test, df = 14, $P = 0.017$), indicating that the northern populations have fewer alleles per locus. I computed heterozygosity values by direct count. The values for the different islands fall between 0.000 and 0.292 (Table 4). When the heterozygosity values are divided into the northern and southern populations, the mean heterozygosity per population is 0.104 (SE 0.017)

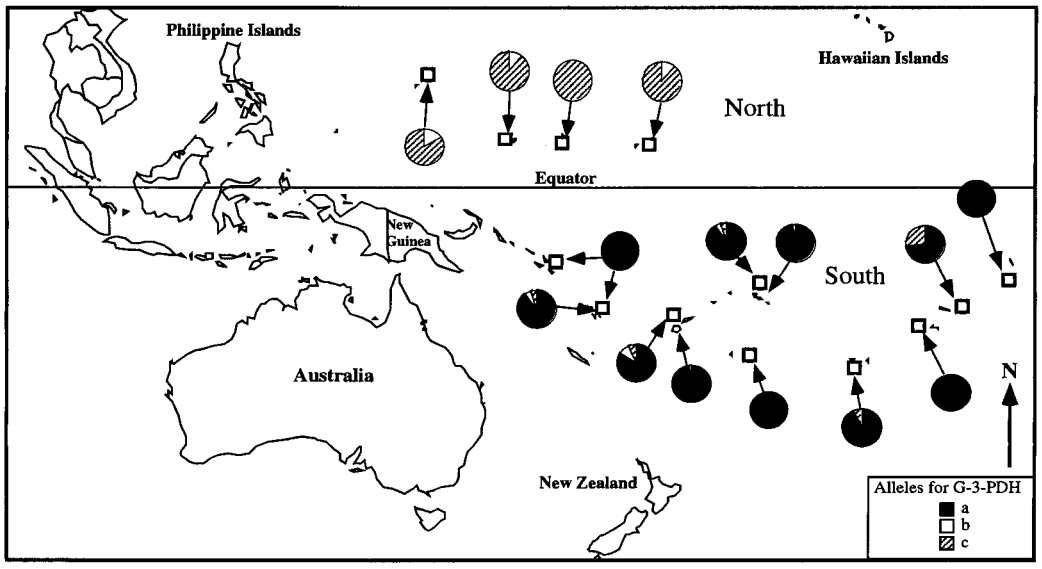

FIG. 4. Allelic frequencies for G-3-PDH for *Gehyra oceanica*.

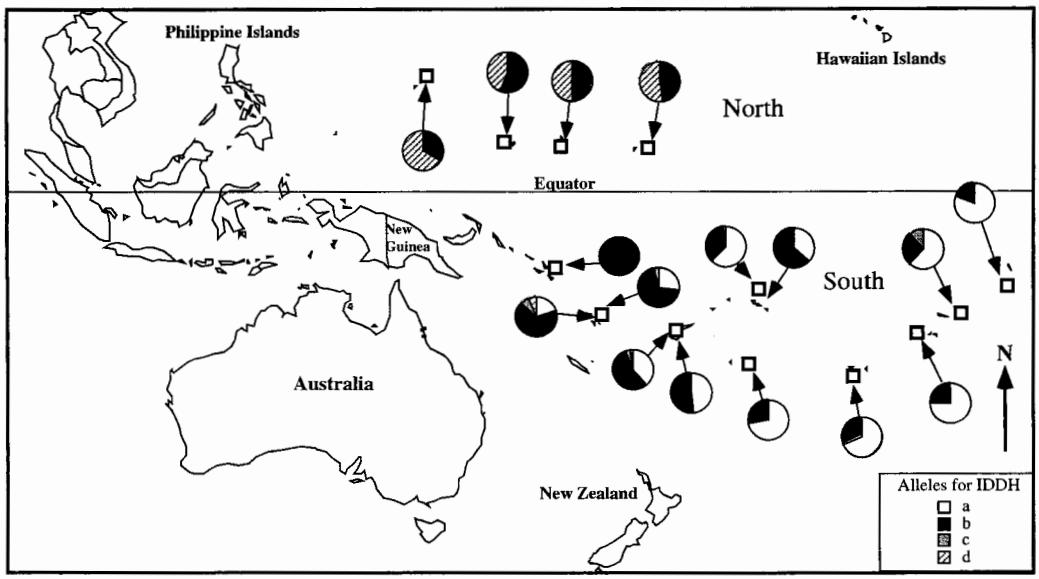

FIG. 5. Allelic frequencies for IDDH for *Gehyra oceanica*.

for the north, and 0.203 (SE 0.023) for the south. These sets of populations are significantly different (t-test, df = 14, P = 0.032), thus the southern populations have almost twice the average heterozygosity of the northern ones. The northern populations are less variable for both of these estimates of genetic variability than the southern populations. If these estimates of genetic variability are divided as in Figure 1, representing the human pattern, then the western populations and the eastern populations are less different than when divided north and south (average alleles per locus: western populations 2.00, eastern populations 1.63; heterozygosity: western populations 0.183, eastern populations 0.181).

The genetic distance matrix (Table 5) based on Nei's (1978) unbiased genetic distance was used to produce a UPGMA phenogram (Fig. 6). There are two well-defined clusters that identify a northern population and a southern population. The southern population is further broken into three other general clusters: east, central, and west. The mean genetic distance (± SE) between populations in the north and those in the south is 0.341 ± 0.007, whereas the mean among the south is 0.045 ± 0.005 and among the north is 0.000. These results support that *G. oceanica* is divided into very different northern and southern forms, even though the northern populations are geographically much closer to some southern populations than the southern ones are to many other southern populations. I did not compare the genetic distances in my study to other published studies, because my values are inflated since I did not include monomorphic loci in the analysis. When I combined populations, and when I further subdivided my populations (see Methods), to produce other UPGMA phenograms based on the different genetic distances, the result was basically the same as illustrated in Figure 6. There was always the north to south division, and a west to east

TABLE 5. Estimates of genetic distance (Nei [1978] below diagonal, and Rogers [1972] above) for five polymorphic loci for 16 island populations of *Gehyra oceanica*.

	Island															
	SOLO	VAEF	VAEM	FIJI	BEQA	TONG	WSSA	WSUP	COOK	SOCI	TUAM	MARQ	MARS	KOSR	POHN	ROTA
SOLO		0.107	0.063	0.167	0.201	0.220	0.192	0.146	0.333	0.270	0.226	0.262	0.361	0.367	0.345	0.386
VAEF	0.010		0.060	0.100	0.153	0.185	0.130	0.112	0.265	0.224	0.165	0.246	0.352	0.359	0.339	0.373
VAEM	0.010	0.000		0.114	0.148	0.167	0.139	0.093	0.280	0.217	0.173	0.210	0.350	0.356	0.337	0.371
FIJI	0.048	0.020	0.015		0.082	0.119	0.069	0.073	0.195	0.155	0.124	0.180	0.304	0.313	0.295	0.320
BEQA	0.076	0.040	0.033	0.008		0.109	0.095	0.057	0.135	0.106	0.156	0.165	0.370	0.378	0.362	0.383
TONG	0.139	0.079	0.063	0.024	0.018		0.082	0.147	0.130	0.059	0.144	0.069	0.354	0.363	0.351	0.360
WSSA	0.100	0.044	0.034	0.008	0.008	0.002		0.090	0.153	0.111	0.077	0.142	0.349	0.358	0.344	0.357
WSUP	0.037	0.014	0.010	0.004	0.000	0.036	0.015		0.190	0.148	0.144	0.207	0.361	0.369	0.351	0.379
COOK	0.186	0.122	0.114	0.050	0.017	0.020	0.030	0.047		0.091	0.206	0.141	0.415	0.424	0.411	0.422
SOCI	0.164	0.095	0.081	0.036	0.016	0.000	0.008	0.041	0.000		0.163	0.085	0.409	0.419	0.407	0.414
TUAM	0.126	0.054	0.051	0.022	0.029	0.019	0.001	0.035	0.050	0.028		0.198	0.332	0.341	0.329	0.339
MARQ	0.187	0.118	0.098	0.047	0.038	0.002	0.017	0.066	0.025	0.000	0.036		0.366	0.375	0.364	0.369
MARS	0.336	0.306	0.338	0.257	0.350	0.366	0.324	0.333	0.397	0.415	0.248	0.393		0.027	0.016	0.039
KOSR	0.348	0.321	0.353	0.274	0.366	0.384	0.341	0.349	0.411	0.433	0.256	0.412	0.000		0.033	0.067
POHN	0.309	0.288	0.318	0.242	0.334	0.357	0.313	0.315	0.385	0.406	0.239	0.387	0.000	0.000		0.056
ROTA	0.374	0.328	0.364	0.273	0.367	0.372	0.333	0.355	0.408	0.421	0.258	0.394	0.000	0.000	0.000	

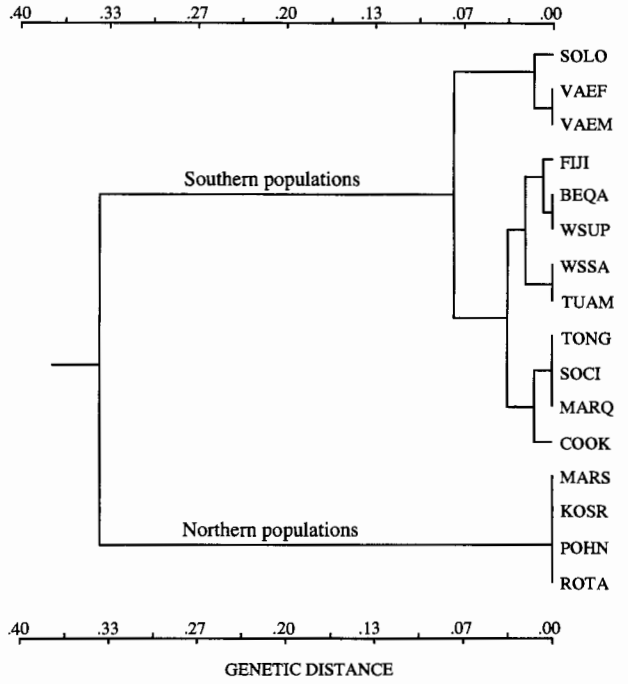

FIG. 6. UPGMA cluster analysis of Nei's (1978) genetic distances for 16 populations *Gehyra oceanica*. The cophenetic correlation between the distance matrix and the phenogram is 0.967.

pattern across the south, although the branching pattern of some of the southern populations changed.

Estimating Levels of Differentiation.—I computed F_{St} values for the 16 *G. oceanica* populations first, then I recomputed them twice more (with a minimum number of populations [12] and with a maximum population [20] subdivision) to determine whether the pattern within archipelagos would affect the overall levels of gene flow. For all the 16 populations the mean F_{ST} value was 0.266 across loci with *G-3-PDH* and *IDDH* having the highest individual values. These are the only loci that are polymorphic in the northern populations (Table 4), and have a very different distribution of alleles there compared to the southern populations (Figs. 4, 5). When I recomputed the F_{ST} values, they ranged from 0.275 for only archipelagos, to 0.272 for 20 populations total, indicating that the intraarchipelago gene flow is not greatly affecting the overall estimate of F_{ST} across populations.

Next, I calculated the F_{ST} values separately for the northern and southern populations (Table 6). The mean F_{ST} value across loci for the southern populations is 0.093, and for the northern populations is −0.045, compared to the combined value for all populations of 0.266, indicating that there are two subpopulations, and gene flow is higher within the north, and south. The negative value for the northern populations indicates that F_{ST} is not different from 0.000, and gene flow between populations is very high. I reanalyzed the northern populations with the removal from the Marshall Islands population of four individuals that were collected two years after my first collection, to see if there was any effect on F_{ST} across the north, but there was not. The F_{ST} value for *G-3-PDH* went from an F_{ST} value of 0.634 for northern and southern populations combined, to 0.060 for the southern alone (Table 6). This difference is consistent with the fixation of alternative alleles between some of the northern and southern populations (Fig. 4), indicating a lack of gene flow between several populations.

Gehyra mutilata

There are two important results from the allozyme variation. First, the samples from across the Pacific showed no genetic variation for the loci surveyed. There also was no intrapopulation variability found within mainland samples. Second, there are fixed differences at three loci (*IDDH*, *MPI-1*, and *6-PGD*) between southern Asian and Pacific populations (populations 1–11, 13, 15) and other mainland Asian populations (populations 12, 14, 16, 17) (Fig. 7). This appears as a north-south break and in Asia, with a disjunction across the Isthmus of Kra, in Thailand, and another one in the Philippines (Fig. 7). There may be a general vertebrate disjunction across the Isthmus of Kra, with birds showing a strong north to south turnover (Woodruff pers. comm.). The islands that populations 12 and 14 inhabit were connected during the last glaciation, at a lowered sea level, but population 13, on Negros, was never connected with these islands (Brown and Alcala 1970). Individuals inhabiting populations from Negros and southern Thailand are identical with the populations from across the Pacific, for these informative loci, and indicate that the source for the Pacific populations of *G. mutilata* probably came from southern Asia. As there is no genetic variation in the Pacific or southern Asia for these loci, it is not possible to distinguish between the alternate dispersal hypotheses for *G. mutilata* with only molecular data.

TABLE 6. *F*-statistics for *Gehyra oceanica*.

Locus	All populations			Southern only			Northern only		
	F_{IS}	F_{IT}	F_{ST}	F_{IS}	F_{IT}	F_{ST}	F_{IS}	F_{IT}	F_{ST}
CK-1	0.219	0.282	0.079	0.217	0.266	0.063	—	—	—
G-3-PDH-1	−0.004	0.633	0.634	0.022	0.081	0.060	−0.095	−0.111	−0.015
LDH-2	0.076	0.176	0.108	0.073	0.148	0.082	—	—	—
6-PGD-1	−0.013	0.059	0.072	−0.016	0.056	0.071	—	—	—
IDDH-1	0.104	0.282	0.198	0.034	0.152	0.122	0.458	0.427	−0.057
Weighted mean*	0.095	0.336	0.266	0.069	0.156	0.093	0.311	0.279	−0.045
Standard error**	0.012	0.082	0.054	0.016	0.058	0.009	0.195	0.138	0.015

* From Weir and Cockerham 1984.
** Calculated by jackknifing across loci (Weir and Cockerham 1984).

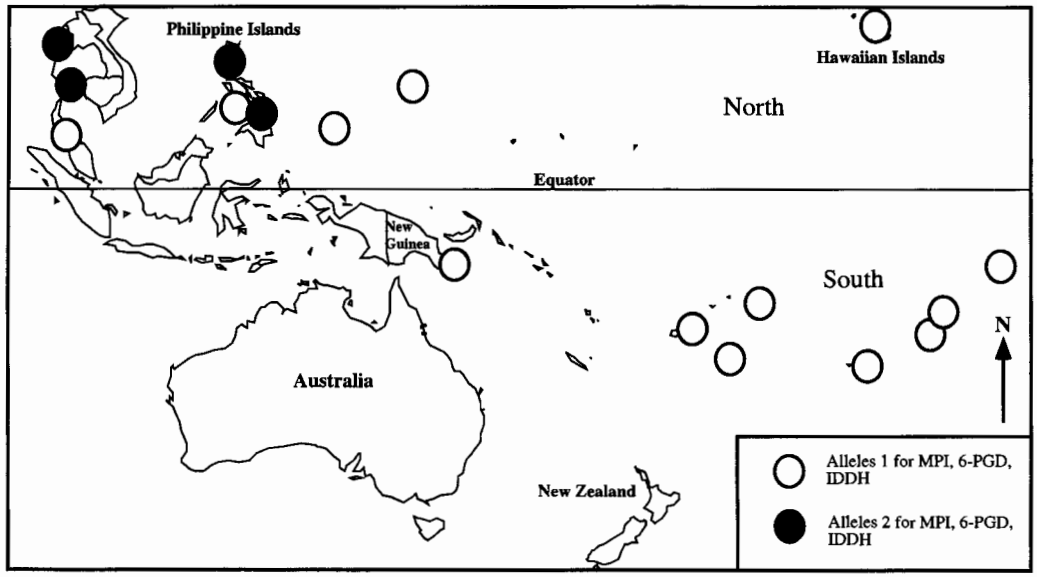

FIG. 7. Allelic frequencies for *Gehyra mutilata*.

DISCUSSION

Comparison of Genetic Results for the Two Gehyra Species

The two *Gehyra* species differ in their genetic variation. *Gehyra oceanica* has genetic variation (Table 4), whereas *G. mutilata* had no discernible genetic variation in the Pacific (Fig. 7). *Gehyra oceanica* has significant differences in heterozygosity and the number of alleles per locus between populations north and south of the equator. Table 7 compares percent polymorphic loci and heterozygosity levels between natural lizard populations and populations of these species that were introduced recently to islands. These data indicate that six of seven times the introduced populations have lower heterozygosity values than do the source populations, and that all seven species have decreased polymorphism in the introduced populations. The northern populations of *G. oceanica* have have reduced genetic variation, compared to the southern populations, that might be consistent with a historic genetic bottleneck (Leberg 1992) as shown in other lizards (Table 7). All the alleles present in the north are a subset of those in the south (Table 4), indicating the southern populations could be the source pool for the north, if a propagule could have successfully traversed the equatorial barrier. It is more likely that the southern populations have maintained a higher allelic diversity if both the northern and southern populations had their source in the Bismarck archipelago. The hypothesis that populations in the northern Solomons and the Bismarcks represent a third and more primitive population of *G. oceanica* was suggested by Beckon (1992). This hypothesis could be tested with DNA sequence data from these different areas to determine whether the northern and southern populations are sister taxa, or if one is the sister taxon to populations in the Bismarcks, if that is the source area and consistent with Beckon (1992).

Pacific populations of *G. mutilata* had a lack of any genetic variation, in my study, therefore $F_{ST} = 0$, which is higher overall than that measured in *G. oceanica*. Table 8 compares the F_{ST} values for *G. oceanica*, from my study, to those for all other published lizard studies. The values presented in Table 8 for F_{ST} from the literature are based only on polymorphic loci. The combined northern and southern population values are higher than those of all within-species values for lizards (Table 8), indicating that there is little or no gene flow between these areas as a result of strong population subdivision. This is consistent with the morphological difference observed by Beckon (1992) in preanal-femoral pore counts between northern and southern populations, and evidence that there may be cryptic species within *G. oceanica*.

TABLE 7. Comparison between native and introduced populations of lizards for genetic variation parameters.

Species*	Years since introduction	# loci	% Polymorphic loci		Proportion decline	Heterozygosity		Proportion decline
			Source	Introduced		Source	Introduced	
Anolis aeneus	—	23	0.230	0.130	0.43	0.035	0.035	0.00
Anolis extremus	>30	21	0.290	0.072**	0.75	0.043	0.006**	0.86
Anolis grahami	70	24	0.500	0.290	0.42	0.078	0.064	0.18
Anolis leachei	>30	22	0.335	0.090	0.73	0.069	0.040	0.42
Anolis richardi	—	23	0.220	0.170	0.23	0.049	0.031	0.37
Anolis trinitatis	—	22	0.410	0.045	0.89	0.068	0.001	0.98
Trachydosaurus rugosus	<150	17	0.470	0.412	0.12	0.133	0.120	0.11

* Data for first six species from Gorman et al. (1978), last species from Sarre et al. (1990).
** Mean of two introduced populations.

TABLE 8. Comparison of all F_{ST} values published for lizards.

Species	Localities	F_{ST}	Source
Northern only (G.o.)	island	−0.045	This study
Egernia modesta	mainland	0.038	Milton 1990
Trachydosaurus rugosus	mainland	0.046	Sarre et al. 1990
Egernia whitii	mainland	0.050	Milton 1990
Lampropholis couperi	mainland	0.064	Mather and Hughes 1992
Gehyra variegata	mainland	0.064	Moritz 1992
Lampropholis delicata	both	0.072	Mather and Hughes 1992
Southern only (G.o.)	island	0.093	This study
Petrosaurus thalassinus	both	0.108	Aguilars-S. et al. 1988
Sceloporus grammicus	mainland	0.135	Aguilars-S. et al. 1988*
Podarcis wagleriana	island	0.153	Capula 1994
Trachydosaurus rugosus	island	0.185	Sarre et al. 1990
Gehyra nana	mainland	0.202	Moritz 1992
Lampropholis adonis	mainland	0.226	Mather and Hughes 1992
Sceloporus graciosus	mainland	0.231	Thompson and Sites 1986
Uta stansburiana	mainland	0.232	Wright 1978**
All poplulations (G.o.)	island	0.266	This study

* Modified from Sites and Greenbaum 1983.
** Data from McKinney et al. 1972.

Values derived for the northern and southern populations individually indicate a very low F_{ST} for the northern populations (not different from zero), thus very high levels of gene flow between northern populations. This value is lower than all values reported for other lizards in the literature (Table 8); further, this may result from a recent range expansion from a single population, or a genetic bottleneck. The southern populations have a lower level of F_{ST} than the total for all *G. oceanica* populations, but it falls within the range recorded for Australian species of *Gehyra* and within lizards in general (Table 8). The southern populations have similar gene flow patterns as noninsular species, probably due to natural dispersal, and the maintenance of gene flow, without the aid of humans.

The contrast between the two *Gehyra* species indicates that very different mechanisms of dispersal are in action. *Gehyra mutilata* is invariant across the Pacific for the loci resolved, which is consistent with the human dispersal hypothesis of a colonization from only a few founders. Although when mainland populations were sampled for allozymic variation there was none, implying the genetic bottleneck had occurred in Asia; but two different types of *G. mutilata*, a northern mainland type and a southern mainland type, were distinguishable based on fixed allelic differences at three loci in Asia (Fig. 7). Thus a bottleneck may have occurred in Asia prior to the dispersal of the Pacific populations. Nei et al. (1975) estimate that it could take tens of millions of years to recover from a severe bottleneck, therefore the bottleneck could have occurred even prior to humans living in Asia. Nevertheless, the southern mainland type is identical to the Pacific populations, which suggests that the movement of proto-Polynesians was from the southern region, if *G. mutilata* was transported with them. Data from mitochondrial DNA (mtDNA) could be very informative regarding the colonization sequence across the islands, as it has a more rapid rate of evolution (Wade et al. 1994). Wade et al. (1994) present evidence that mtDNA diversity should decrease more rapidly that allozymic variability during bottlenecks, and Shaffer and Stanley (in prep.) show that cryptic patterns of population relationships may be resolved only with mtDNA data. Therefore, mitochondrial DNA could discriminate between Asian *G. mutilata* populations that might have experienced a bottleneck initially millions of years ago, and those populations recently established from these sources. The species *G. oceanica* shows natural levels of gene flow between southern populations, when compared to published values calculated for other lizard species. Although there is the possibility this pattern is caused by human transport, the strong north-south split in the data is evidence for the natural dispersal hypothesis and agrees with Beckon's (1992) findings. Data from mitochondrial DNA might confirm this pattern, or a pattern consistent with other genetic bottlenecks, not apparent with allozymes.

How Did Gehyra mutilata Disperse across the Pacific?

The genetic pattern of no variation in *Gehyra mutilata* is consistent with human or natural dispersal, but evidence from its life history and Pacific distribution support that the human pattern is probably correct. If *G. mutilata* is dispersing with humans, it could be transported as either eggs or adults. The eggs of *G. mutilata*, as with other species of *Gehyra*, are cleidoic (calcified) and do not need environmental water (Bustard 1968); thus, once they are laid, they develop with little or no gas exchange across the shell. *Gehyra mutilata* eggs have been shown to survive sea water exposure of up to 11 days (Brown and Alcala 1957), and their incubation requires 57–65 days (Gibson-Hill 1950; Chou 1979). A recent test of the speed at which Polynesians were able to cross the large oceanic barriers between islands was accomplished with a traditional canoe traveling between Hawai'i and Tahiti (Bellwood 1979). This trip took 35 days and traversed almost 5000 km against the sea currents (Bellwood 1979). Therefore it seems plausible that *G. mutilata* eggs could make such a voyage as stowaways. Alternatively, adults may have been transported in sailing ships, as these ships may be 18 meters long and carry considerable cargo (Bellwood 1979). This species is shown to be closely associated with urban settings across the Pacific and the likelihood of its accidental transport is reasonably high, either as adult or eggs (Brown and Alcala 1970; Zug 1991; Fisher, unpubl. data). Because of this association with human settlements, they would have a higher likelihood of establishing populations in areas along frequently traversed routes, such as villages in the Pacific. I postulate that *G. mutilata* were dispersed with proto-Polynesians directly from southeast Asia and that is why their current distribution in Melanesia is very restricted. These proto-Polynesians were supposed to have made coastal contact only in New Guinea and New Britain, then bypassed most of Melanesia (Vanuatu, New Caledonia, and Fiji) to settle in Polynesia from Samoa and Tonga continuing to the

east, and Micronesia in the north. The distribution of *G. mutilata* in Melanesia is consistent with this hypothesis, as it occurs only in scattered, mainly coastal, villages. Further to the east in the region settled by proto-Polynesians, *G. mutilata* occurs on many scattered islands where it occurs in villages on coasts and inland, and in Hawai'i *G. mutilata* occurs commonly in forests and rocky regions away from village settings.

How Did Gehyra oceanica Disperse?

If *G. oceanica* is naturally dispersed across the Pacific, then how were they able to cross the huge water barriers and how do they maintain gene flow? The two alternative hypotheses for lizards in general are either as adults adrift on some vegetative raft (Darlington 1957; Gibbons 1985; Beckon 1992) or floating of their own means (McCann 1953; Schoener and Schoener 1984); or alternatively as a cache of eggs in a dead *Pandanus* aerial root, or other raft (Wallace 1881; Brown and Alcala 1957; Gardiner 1984). *Gehyra oceanica* are large (100 mm SVL and 17 g weight; Zug 1991; Beckon 1992) lizards and could survive a long period of time floating as adults on a raft without food or water. There would have to be either frequent propagules to colonize a single island, many adults traveling together on a single raft, or one gravid female to establish a new population. Rafts are typically associated with large rivers where mats of vegetation would become entangled and then dislodged during a storm, carrying with it a subset of the forest fauna. I suspect most Pacific island rivers are too small to create these large rafts and that, rather, individual trees are actually dislodged during hurricanes carrying even a smaller fraction of the forest fauna. The likelihood of adults surviving an oceanic trip on an individual tree is probably relatively low.

The egg hypothesis is more likely and dependent on the following observations. First is that *G. oceanica* has communal nests of fewer than ten eggs to several dozen eggs each with individual females laying only two eggs at a time (Gibbons and Zug 1987; pers. obs.) and these nests are frequently in coastal *Pandanus* sp. aerial roots, and the hollow stems of *Scaevola* (Niering 1963; pers. obs.). Second, these eggs have extremely long incubation periods (up to 115 d; Schwaner 1980) and are probably very resistant to sea water exposure as are other Gekkonine eggs (Brown and Alcala 1957; Gardiner 1984). *Gehyra mutilata* eggs have survived constant sea water exposure of up to 11 days, and *Phelsuma*, another oceanic island endemic, eggs survived up to a full day under sea water (Brown and Alcala 1957; Gardiner 1984). Lastly, the annual hurricanes in the tropical Pacific often cause waves high enough to overwash entire atoll islands (Blumenstock 1961). These hurricanes dislodge entire trees (Blumenstock 1961) and if a tree with a communal nest was set adrift there would probably be enough variation in egg incubation time that some eggs would still be unhatched and viable up to three months after it was set adrift. These eggs could serve as a propagule for an uninhabited island or gene flow between unconnected islands. The communal nest probably helps to prevent bottlenecks as multiple females clutches, each with two eggs, are represented and therefore several nonsibling hatchlings might be present to serve as propagules, as opposed to a single, or few adults on a tree. This mechanism could maintain both nuclear and mtDNA diversity, as individual adults can carry only one haplotype and one or two alleles, unless they are gravid females, which could carry up to four alleles; however, in a communal nest each female's eggs might have a different haplotype and four different alleles could be present for each clutch (Wade et al. 1994). If the populations of *G. oceanica* across the Pacific have high mtDNA haplotype diversity, then the communal nest hypothesis may be correct, or gene flow could be great enough to maintain the diversity.

Rawlinson et al. (1990) reviewed the history of the colonization of Krakatau Islands (Indonesia) over the 100-year period since volcanic eruptions destroyed all vertebrate life on these islands. They show that during this period a minimum of six gecko species were able to colonize these islands by crossing the 44-km channel from source populations on Java and Sumatra (Rawlinson et al. 1990). If this estimate is representative of the colonization ability of geckos in general, then their natural chance dispersal across the Pacific Basin islands over a period of thousands to millions of years does seem plausible, as does gene flow between certain island groups thus maintaining low values of F_{ST}, as seen in the northern *G. oceanica* populations.

The natural north and south genetic division in *G. oceanica* is predicted by the ocean currents as both directly north and directly south of the equator is a zone where there is no current and the sea is calm. Right outside this zone, both north and south currents head from the east to the west making it hard or impossible for species to drift across this zone (Fig. 2; Nunn 1994). The annual hurricanes that occur in the Pacific, representing over 60% of the global tropical storms, are generally absent from 5°N to 5°S of the equator due to persistent high pressure (Nunn 1994). Hence, the equator is a very effective barrier to natural gene flow, as neither oceanic currents or hurricanes operate in a north/south fashion. Once a species does cross this barrier it would probably have low or no continued gene flow across the barrier.

Relevance of the Dispersal Hypotheses to Pacific Island Gecko Biogeography

The gekkonid fauna of the majority of the Pacific Basin is composed of four widespread parthenogenic species (*Lepidodactylus lugubris*, *Hemidactylus garnotii*, *Hemiphyllodactylus typus*, and *Nactus pelagicus*), four species of *Gehyra*, and 24 other sexual species of geckos in eight genera (Table 9). Recently, the evolution of all four parthenogenic and four sexual species has been analyzed with molecular techniques (Moritz 1987; Moritz et al. 1993; Donnellan and Moritz 1995; Radtkey et al. 1995; Zug, pers. comm.). These studies indicate that three of the four parthenogenic species each had one origin in the Pacific or Southeast Asia, and that there is little or no variation in the Pacific populations (Moritz 1987; Moritz et al. 1993; Zug, pers. comm.). The fourth parthenogenetic species analyzed (*L. lugubris*) apparently had its origin in the Pacific Basin (Radtkey et al. 1995), and it is quite variable for a parthenogenic species (Moritz et al. 1993; Radtkey et al. 1995). *Gehyra mutilata* is similar to *H. garnotii*, *H. typus*, and *N. pelagicus*, the three parthenogenetic species,

TABLE 9. Distribution of geckos on oceanic Pacific archepelagos. Three categories of species are present: E = endemic to oceanic islands; W = occur also in New Guinea, or Philippines; I = species known to be introduced since 1940. Data taken from Zug 1991, and pers. obs. of field and museum specimens.

	North Pacific					South Pacific						
Species	Belau	Carolines	Marshalls	Marianas	Hawai'i	Solomons	Vanuatu	Fiji	Tonga	Samoa	Cooks	French Polynesia
Parthenogenetic												
Lepidodactylus lugubris	W	W	W	W	W	W	W	W	W	W	W	W
Nactus pelagicus		E	E	E			E	E	E	E	E	E
Hemiphyllodactylus typus					W		W	W	W		W	W
Hemidactylus garnotii					W			W	W	W	W	W
Sexual												
Hemiphyllodactylus typus	W											
Gehyra brevipalmata	E											
Gekko n. sp.	E											
Lepidodactylus paurolepis	E											
Perochirus scutellatus	E	E										
Lepidodactylus moestus	E	E	E									
Perochirus ateles		E	E	E								
Phelsuma laticauda					I							
Gehyra mutilata	W	W		W	W	W	W	W	W	W	W	W
Gehyra oceanica	?*	E	E	E		E	E	E	E	E	E	E
*Hemidactylus frenatus***	W	I	I	W	I	I	I	I	I	I	I	I
Lepidodactylus n. sp.***			E								E	E
Cyrtodactylus biordinus						E						
Cyrtodactylus louisidensis						W						
Lepidodactylus flaviocularis						E						
Lepidodactylus guppyi						E						
Lepidodactylus mutahi						E						
Lepidodactylus shebae						E						
Lepidodactylus woodfordi						W						
Gekko vittatus						W	W					
Nactus multicarinatus						E	E					
Lepidodactylus n. sp.							E					
Perochirus guentheri							E					
Gehyra vorax							E	E				
Lepidodactylus gardineri								E				
Lepidodactylus manni								E				
Lepidodactylus euaensis									E			
cf *Perochirus* sp.****									E			

* Apparently has recently arrived in Belau (Fisher, pers. obs.; Crombie, pers. comm.)

** Recently has colonized most of the Pacific (Moritz et al. 1993; Petren et al. 1993; Case et al. 1994); records for the Carolines (1991), Marshalls (1991), and Cooks (1994) were first made by Fisher (unpubl. data).

*** Records are from Radtkey et al. (1995).

**** Pregill 1993.

because it is invariant across the Pacific for the allozyme loci resolved (Moritz 1987; Moritz et al. 1993; Zug, pers. comm.). In total, the parthenogenic species are not well suited to test the importance of human-mediated dispersal in the Pacific, because individual females are able to serve as propagules to colonize new islands. Parthenogenic species resulting from one founding will be identical wherever they occur, thus obscuring their history of colonizations. The species *L. lugubris* is the only parthenogenic species that has multiple major clones in the Pacific; however, most of these have a wide overlapping distribution, thus obscuring their historical distributional pattern (Moritz et al. 1993; Radtkey et al. 1995).

Of the four sexual species studied previously, two are species of *Lepidodactylus*, one is *Nactus multicarinatus* that probably consists of several allopatric biological species in New Guinea and the western Pacific (Moritz 1987; Donnellan and Moritz 1995; Zug and Moon 1995), and the other sexual species, *Hemidactylus frenatus*, is known to have been introduced by humans after World War II (Moritz et al. 1993; Petren et al. 1993; Case et al. 1994). The samples of *H. frenatus* were shown to have strongly differentiated mtDNAs, even in sympatry, and not much allozyme variability, thus indicating that important variation occurs in the Pacific, probably resulting from multiple sources in Asia (Moritz et al. 1993). Since *H. frenatus* has been present in the Pacific only for 50 years, this information will be of limited value in understanding the role of pre-Europeans in Pacific Island biogeography. The two species of *Lepidodactylus* are relevant to the genetic pattern seen in *G. oceanica*. The first species is *Lepidodactylus moestus,* which occurs across Micronesia, like the northern populations of *G. oceanica* (Ota et al. 1995; Radtkey et al. 1995; Table 9). This species was studied with allozymes and mtDNA, and has very low heterozygosity (0.005) and only one of 17 loci was polymorphic (Hanley et al. 1995), but each of five individuals that were sequenced for mtDNA had unique haplotypes with three present on one

island (Radtkey et al. 1995). Therefore it is possible that both species of *Gehyra* might be maintaining a high mtDNA diversity even in the absence of allozyme diversity. This would be consistent with Shaffer and Stanley (in prep.), but contrary to Wade et al. (1994). The second species is a very specialized undescribed species of *Lepidodactylus* apparently restricted to beaches on atolls (Ineich and Ota 1993; Hanley et al. 1994; Radtkey et al. 1995). This species occurs north and south of the equator, and a population in the north and one in the south have each been characterized for allozyme variation, and one individual from each was also sequenced for mtDNA (Radtkey et al. 1995). The levels of allozyme variation found are similar to those for *L. moestus* within each population, but there are frequency differences between the two populations for two loci, and the mtDNA is different for both individuals across the equator (Radtkey et al. 1995) indicating that this may be a natural phenomenon.

The distribution of geckos across the Pacific Basin (Table 9) shows that of the 26 sexual gecko species (not including the recent invaders *H. frenatus*, or *Phelsuma laticauda*), seven occur only in the north and 16 occur only in the south. Only three occur both in the north and south; two of these are the *Gehyra* species and the third is the undescribed species of *Lepidodactylus*. The distributions of the geckos illustrate the difficulty in naturally crossing the equatorial currents. Humans, on the other hand, have apparently been able to cross without difficulty, and therefore human commensals should be genetically the same across this barrier, whereas natural species might show this disjunction in gene flow. Figure 6 shows that *G. oceanica* is genetically disjunct across the equator.

If the equatorial currents are an effective barrier to gene flow in geckos, then this should be reflected in the other widespread family of lizards in the Pacific, the Scincidae, but not necessarily in air dispersers such as birds and bats. Therefore, we should not expect similar distributions between air- and water-dispersed species (Carlquist 1981). The skinks (Scincidae) are represented by four species occurring widely both north and south of the equator, four other species that are widespread in New Guinea and occur only in a few populations in the north and south, but all other species occur exclusively only north (14) or south (48) of the equator on the oceanic islands. Of these four widespread species, *Cryptoblepharus* sp. and *Lipinia noctua* are unstudied genetically from across the Pacific (*Lipinia* has been studied in New Ireland; Austin 1995), although they have been studied morphologically. Zweifel (1979) studied the morphology of *L. noctua*, and concluded that it is geographically uniform across the Pacific, but it appears that this morphological conservatism may not represent genetic conservatism (Austin 1995), and when many of these populations were seen in life, they have color differences that are lost in preservative (pers. obs.). Mertens (1931) and Zug (1991; pers. comm.) have looked at the morphology of different populations of *Cryptoblepharus* from across the Pacific and find that several can be diagnosed from the rest, and are currently considered separate allopatric species. The best support for the equatorial barrier to gene flow comes from a study conducted by Bruna et al. (1996) that looked at the genetics of the two widespread *Emoia* species (*cyanura* and *impar*) and found that *E. cyanura* had a phylogeographic pattern similar to *G. oceanica*, but *E. impar* did not; therefore they are split in their support of the importance of the equatorial currents in Pacific island lizard distributions.

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