Molluscs of the Northern Mariana Islands, With Special Reference to the Selectivity of Oceanic Dispersal Barriers[1]

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Abstract—The shelled molluscan fauna of the Northern Marianas, a chain of volcanic islands in the tropical western Pacific, consists of at least 300 species. Of these, 18 are unknown from or are very rare in the biologically better known southern Marianas. These northern-restricted species are over-represented among limpets and in the middle to high intertidal zones of the northern Marianas. At least 22 gastropods which are common in the intertidal zone and on reef flats of the southern Marianas are absent in the northern Marianas.

The northern Marianas lie within the presumed source area of the planktonically derived part of the Hawaiian marine fauna. The ocean barrier between the northern Marianas and the Hawaiian chain appears to select against archaeogastropods and against intertidal species but is unselective with respect to adult size and to other aspects of gastropod shell architecture. These findings are consistent with those for other dispersal barriers.

Introduction

The Mariana Islands form the southern part of an island chain which extends northward through the Bonin, Volcano, and Izu Islands to central Honshu, Japan. Whereas the marine biota of the southern Marianas (Guam, Rota, Tinian, and Saipan) is becoming relatively well known, that of the northern Marianas (Fig. 1) is largely unstudied. Besides a few scattered records, the only published marine biological accounts are those of Tsuda and Tobias (1977a, b), who provided a checklist of algae.

The taxonomic composition and biogeographical affinities of the marine fauna of the northern Marianas are interesting for at least three reasons. First, the shores of the northern islands are almost entirely volcanic and might be expected to yield species that are absent from the raised limestone and associated reef-flat shorelines of the southern Marianas. Second, the Marianas lie in what has traditionally been

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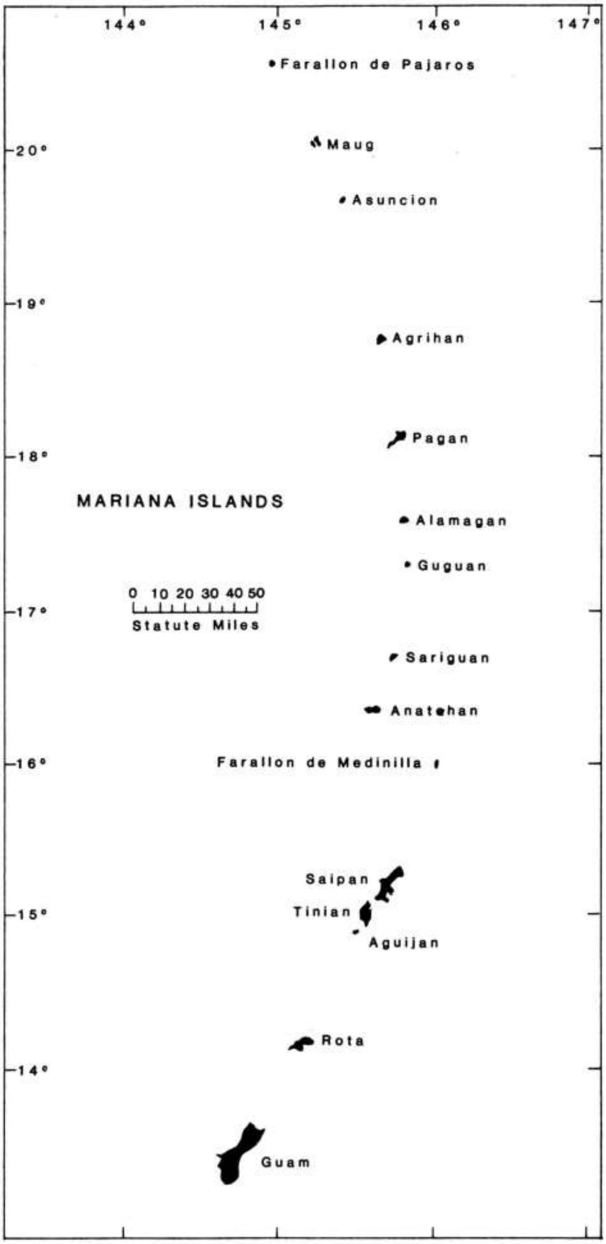

Fig. 1. Map of the Mariana Islands.

considered a source area for the fauna of the Pacific islands which lie to the east of the Indo-Malayan archipelago (Ekman, 1953; Kay, 1984). Thirdly, the northern Marianas lie on the eastern edge of the Philippine plate, separated from the Pacific plate on which most of the islands of the Pacific lie, by the deep Marianas Trench, and thus are a test area for some of the biogeographical hypotheses recently proposed by Kay (1980a, 1984) and Springer (1982).

The molluscan fauna of the northern Marianas especially invites comparison with that of the Hawaiian Islands which, like the northern Marianas, are largely volcanic. The Hawaiian chain consists of a series of 26 islands extending from Hawaii in the southeast, the youngest at -1 my, to Kure, an atoll resting on an ancient volcanic pedestal to the northwest. Dating of basalt at Midway near Kure indicates that the island was above the sea in the Miocene, 30 my ago (Ladd et al. 1970). The age sequence in the Mariana Islands is opposite that in Hawaii; Guam and Saipan in the south are the oldest islands and much of their volcanic base is capped with Pliocene and Pleistocene limestone. The northern arc of islands, from Anatahan to Uracas, is a series of young volcanic islands, and Pagan, Asuncion, and Uracas are all active volcanoes.

The subtropical countercurrent, which arises in the west as an offshoot from the Kuroshio Current, flows eastward through the northern Marianas and continues erratically eastward to Johnston Island and thence to the northwestern Hawaiian islands. (For discussions of the biogeographical affinities of the Hawaiian Islands see Kay, 1967, 1980a; and Grigg, 1981.) The fauna of the northern Marianas thus affords the opportunity to examine the selectivity of the dispersal filter between the Hawaiian biota and its presumed source in the northwestern Pacific.

Very little is currently known about the ecological and architectural differences between widely dispersing and poorly dispersing species. The topic is important because wide dispersal is associated with long-term resistance to extinction (Stanley, 1979). If statistical associations exist between dispersability and biotic competence, long-term evolutionary trends toward an increase in biotic competence might be tied to the evolution of large-scale dispersal by planktonic stages.

Materials and Methods

The material reported on results from several expeditions to the northern Marianas organized by the University of Guam Marine Laboratory between 1972 and 1981. All three of us have made field observations in the northern Marianas and all nine islands have been visited by one or another of us.Shallow-water habitats were sampled by wading, snorkeling, and scuba diving. Sediment samples collected from tidepools and offshore to depths of 30 m were examined for micromolluscs (molluscs less than 7 mm in greatest dimension) and quantitative analyses were performed following the method of Kay (1980b). We have also examined the collections made by C. Carlson and P. J. Hoff aboard the WANDERER and those of the National Museum of Natural History, Smithsonian Institution (USNMNH).

The shelled molluscs reported on are deposited in the University of Guam Marine Laboratory collection, in the Vermeij collections, and in the Kay collections at the University of Hawaii.

Only species with shells greater than about 10 mm in greatest dimension are used for the analyses of architectural differences among shells. Thick-lipped shells are those which have an expanded or thickened rim of the aperture in the adult stage; thin-lipped shells are those which lack this modification. Species referred to the intertidal are those found in the intertidal and include species which occur both in the intertidal and the subtidal.

Results

Northern Mariana-Southern Mariana Comparison.

A list of species and their occurrence on the nine northern Mariana Islands is presented in Appendix 1. We have excluded small alga-dwellers such as the Eatoniellidae and Cingulopsidae and the sessile Vermetidae (except for *Serpulorbis variabilis*) from our list, and our inventory of the fauna is certain to be incomplete in other respects. However, it shows clearly that several species which are abundant on the shores of Guam and others of the southern Marianas are conspicuously rare or absent in the northern Marianas and vice versa.

Twenty-two common shallow-water, hard-bottom molluscs from Guam which are absent from the northern islands are listed in Appendix 2. Eight (36%) are confined to the middle or high intertidal zones, and 14 (64%) are found chiefly or exclusively on reef flats. It is interesting that *Trochus niloticus* has not been found in the northern Marianas. This species was introduced from Belau (formerly Palau) to Saipan in the late 1930s and to Guam about two decades later (Eldredge, in press). It is now abundant on reef-flats and subtidally to a depth of at least 12 m (B. Smith, pers. comm.) on both Saipan and Guam.

Several other species which are abundant on Guam are found only sporadically in the northern Marianas; others may have been erroneously recorded from these islands. Only one specimen of *Cerithium columna* was found in the northern islands (at Pagan in 1981), and it differs from the abundant intertidal form at Guam by having much finer sculpture. Seven species in the USNMNH collections made by U.S. Armed Forces in 1945 (Appendix 1) have not been found during the University of Guam Marine Laboratory expeditions, and the locality data accompanying the specimens may be erroneous.[1] We have identified 18 species from the northern Marianas which are absent or very rare in the biologically better known southern

[1] A. H. Banner (pers. comm. to GJV, 28 June 1984) tells us that molluscs which he collected at Agrihan and Maug in 1945 were very likely intermixed with material taken at Saipan when a large military truck drove accidentally over the collected specimens. Although he attempted to salvage the remains, Banner cannot guarantee the accuracy of the locality data of the molluscs, which were subsequently deposited at the USNMNH. Species which we believe are erroneously recorded from the northern islands in this way include *Cerithium nodulosum*, *Cymatium nicobaricum*, *C. muricinum*, *Chicoreus brunneus*, *Cantharus fumosus*, *Nebularia chrysalis*, and *Vasum turbinellus*. All these species are common on the reef flats of the southern Marianas including Saipan. We also doubt the record of *Trochus maculatus*, a species probably absent from the southern Marianas.

Marianas (Appendix 1).

Although *Pusia* sp. may be easily overlooked because their shells are less than about 10 mm in greatest dimension, the other species have prominent shells, and we do not believe their absence or rarity on Guam is an artifact of collection. Additionally, several northern Marianas species are reported from Guam but have not been found in recent years. *Haliotis ovina* and *H. varia varia* were recorded by Talmadge (1963). *H. ovina* is represented in the USNMNH collections by one specimen from Saipan. *Nodilittorina pyramidalis* is recorded by Rosewater (1970) from "Apra Bay" (Guam) and from Saipan, but we have not found it in the southern Marianas. *Planaxis niger*, abundant in the northern Marianas, was collected from northern Saipan (Kropp, pers. comm.), but no other southern Marianas record of this species is known.

Most (66%) of the northern-restricted species were found on two or more of the nine islands (Appendix 1). They are particularly well represented in the intertidal zone. Of the 35 gastropod species found in or above the middle intertidal barnacle (*Tetraclita*) zone, 10 (29%) belong to the northern-restricted group. An additional species, *Nerita guamensis*, occurs at two of the northern islands as a dark form which is unknown from the southern Marianas. Species with a limpet-like form comprise 8% of the northern Marianas gastropod fauna as a whole but 29%of the northern-restricted species.

Northern-restricted species are not confined to the Mollusca. Among corals, *Leptastrea* sp. and *Millepora foveolata* are known from Pagan but not from the southern Marianas (R. H. Randall, pers. comm.). At least two porcellanid crabs are northern-restricted (R. K. Kropp, in prep.). The high intertidal hermit crab *Calcinus seurati* has been found at Pagan and Saipan but is unknown from Guam (D. S. Wooster, pers. comm.). The fishes *Labroides pectoralis* and *Pseudodax molluccanus* are also absent from Guam but have been seen at Pagan (R. Myers, pers. comm.). Randall (1982) reports that the surgeon fish *Acanthurus leucopareius*, rare at Guam, is common in the northern Marianas. Algae found in the northern but not the southern Marianas include the phaeophytes *Dictyota hamifera*, *Hormophyta triquetra*, and *Stipopodium hawaiiense* (Tsuda and Tobias, 1977a; Eldredge et al., 1977) and the rhodophytes *Dermonema frappieri*, *Polysiphonia sacchorhiza*, *Laurencia succisa*, *L. surculifera*, *Galaxaura filamentosa*, *G. hystrix*, and *G. veprecula* (Tsuda and Tobias, 1977b; Itono, 1980).

Northern Marianas-Hawaiian Comparison.

Data comparing the molluscan faunas of the northern Marianas and the Hawaiian Islands are set out in Tables 1–3. The northern Marianas Archaeogastropoda (superfamilies Pleurotomariacea, Fissurellacea, Patellacea, and Trochacea) are less well represented in the Hawaiian Islands than are the mesogastropods and neogastropods (Table 1). Indeed, two families of archaeogastropods, the Haliotidae and Acmaeidae, which contribute 17% of the archaeogastropod species to the northern Marianas fauna, are not present at all in Hawaii. The effect of this

Table 1. Hawaiian affinities of the northern Marianas fauna.

	No. of species in northern Marianas	%Occurring in Hawaii
Taxonomic groups		
Archaeogastropoda	41	24
Neritacea	8	50
Mesogastropoda	87	70
Neogastropoda	111	59
Euthyneura	21	33
Polyplacophora	2	0
Bivalvia	39	46
Architectural groups		
* Gastropods, narrow aperture	57	58
* Gastropods, thick or expanded lip	72	68
* Gastropods, thin lip	107	55
* Gastropods, large (>50 mm)	37	51
* Gastropods, small (>10 mm)	53	53
Habitat groups		
Gastropods, middle to high intertidal	35	51
Gastropods, lower shore, hard bottom	122	60
Gastropods, soft bottom	56	52
Bivalves, soft bottom	13	54

* Comparison excluding Archaeogastropoda

Table 2. Numbers of intertidal mollusc species recorded in the northern Marianas and in Hawaii (Hawaiian data from Kay, 1979).

	Northern Marianas	Hawaii
Archaeogastropods	7 (4 families, 6 genera)	3 (1 family, 1 genus all endemic)
Neritidae	6	4
Littorinidae	6	4 (1 endemic)
Planaxidae	2	2
Muricacea	8	9 (2 endemic)
Mitracea	1	2
Smaragdinellidae	1	1
Melampidae	2	6 (2 possibly endemic)
Siphonariidae	2	2
Bivalvia	0	3

Table 3. Numbers of samples and percent species composition of major components of micromolluscan assemblages in the Northern Marianas and in the Hawaiian Islands.

	N. Marianas	Hawaii I.[1]	Oahu I.[2]	Niihau[3]	F. F. S.[4]
No. of samples	19	9	11	6	11
Number shells	3,053	3,032	3,978	2,705	2,334
Percent Composition					
Archaeogastropoda[5]	18	7	3	9	11
Rissoidae	4	23	17	27	18
Cerithiidae	19	3	4	7	13
Dialidae	>1	4	31	9	15

[1] Samples from 3–10 m depth transects on subtidal reef, Kona, Hawaii
[2] Samples from 10 m depth on transects at Waianae, Oahu
[3] Samples from 3–10 m depth on transects on the lee shore of Niihau
[4] French Frigate Shoals. Samples from 8 m depth
[5] Archaeogastropoda do not include *Tricolia variabilis*.

relative lack of archaeogastropods is reflected in two comparisons (Tables 2 and 3). When the numbers of species found in the intertidal in the northern Marianas and the Hawaiian Islands are compared, about the same numbers are found in both areas, but whereas seven species of archaeogastropods occur in the intertidal of the northern Marianas only three archaeogastropod species occur in that zone in Hawaii, all in the same genus (*Cellana*) and all endemic. The numbers of species in other groups are similar for the two island groups, i.e., there are four or five species of nerites, five or six species of littorines, and eight or nine species of muricaceans.

When the relative proportions of micromolluscs from subtidal sediment samples (Table 3) are compared, 18% of the micromolluscs in the samples from the northern Marianas are archaeogastropods (exclusive of *Tricolia variabilis* which is highly variable in numbers both in the northern Mariana and Hawaiian Islands) while in the Hawaiian Islands the figure ranges from 3 to 11%. Rissoids comprise a low proportion of the shells in the northern Marianas but a higher proportion in the Hawaiian Islands, and cerithiids which are also prominent in the northern Marianas (they comprise about 19% of the fauna) are less prominent in Hawaii.

The northern Marianas and Hawaiian marine molluscan faunas are similar in gastropod: bivalve proportions—88 : 12 and 88 : 17, respectively, and the figures for both island groups are consistent with those reported for other islands (Kay, 1967). Soft-bottom and hard-bottom species from the lower shore do not differ in their relative proportions (Table 1). The Hawaiian marine molluscan fauna differs from that of the northern Marianas, however, in its relatively high percentage of endemism at the species level (about 15%, Kay, 1979). There is apparently little or no endemism at this level in the northern Marianas. Several species in the Hawaiian fauna are widespread in the Pacific Ocean and have been termed Pacific plate species (cf. Springer, 1981, 1982; Kay, 1980a, 1984) because they appear to be restricted to the

Pacific plate. In molluscan groups for which there is good distributional information, such as the cowries and strombids, more than 25% of the species in Hawaii are Pacific plate species. We have detected only one cowrie—*Cypraea maculifera* which is predominantly Pacific plate species in the northern Marianas.

With respect to gastropod antipredator shell architecture, mesogastropods, neogastropods, and euthyneura with a narrowly elongated aperture are found in about the same proportion in the northern Mariana Islands and the Hawaiian Islands as are member of these groups with a broad aperture. Furthermore, there are no differences in the proportion of thick-lipped and thin-lipped gastropods exclusive of the Archaeogastropoda (that is, the Neritacea, Mesogastropoda, Neogastropoda, and Euthyneura) in the northern Mariana and Hawaiian Islands. Had we compared the distribution of thick-lipped members of these groups to all thin-lipped gastropods rather than excluding the archaeogastropods, then more thick-lipped, narrow-apertured species would appear. Gastropods of large size (more than 5 cm maximum dimension) are found in Hawaii in the same proportion as are smaller-shelled species (Table 1).

Discussion

The presence/absence and the distribution of molluscs within the northern Marianas are affected by at least three factors: collecting effort, types of habitat, and an island effect, as shown by patchy distributions. More visits were made to Pagan for which the largest number of species was recorded (230) than to other islands of the northern Marianas, and fewer visits were made to Uracas. Pagan is also the most geologically diverse of the islands in the chain, with black sand beaches, raised limestone benches, and subtidal coral communities. Uracas is characterized by a foreshore of basalt boulders and is surrounded by warm sulphurous water. Maug, composed of three weathered volcanic peaks which surround the old crater may have the most extensive coral reef development among the islands. Finally, species presence or absence on all the islands may be the result of an island effect in that the presence or absence of species can be the result of chance. Patchy distributions on islands have been documented for the Line Islands (Kay, 1971) and the Hawaiian Islands (Kay, 1979; 1980a).

Of the occurrences of several species which are abundant on the shores of Guam and others of the southern Marianas but which are absent or rare in the northern Marianas, some are explicable. The absence of species that inhabit seagrass meadows and mangroves is expected because these habitats are not represented in the northern Marianas. For other shallow-water species, however, absence in the north is more puzzling. We rather expected the southern-restricted species to be confined to limestone surfaces and to be absent from volcanic substrates. With the possible exception of the limestone-restricted limpet *Patelloida* sp., however, the southern-restricted species are known from both limestone and volcanic shores. The 22 common shallow-water hard-bottom molluscs from Guam which are absent from the northern islands are ecologically and biogeographically unrepresentative of the fauna as a whole, with over a third of the species confined to the middle and high intertidal zones, and the other two-thirds found on reef flats.

The northern-restricted species are also ecologically, morphologically, and biogeographically atypical of the northern Marianas fauna as a whole, and a high proportion of intertidal and limpet-like forms also characterizes the northern Marianas forms. Additionally, many of the northern-restricted species appear to be confined to high islands and to be absent from atolls. *Usilla fusconigra*, for example, is known from Okinawa, Samoa, the Marquesas, and the Hawaiian Islands, but has not been collected from atolls in the Marshalls, Societies, or Tuamotus (data from USNMNH, British Museum (Natural History), B. P. Bishop Museum). Other examples of high island species include *Cellana toreuma*, the three acmaeids, *Nodilittorina pyramidalis*, and *Planaxis niger*. Some or all of these species may be restricted to volcanic substrates.

The most obvious difference between the Hawaiian fauna and that of the northern Marianas is in the proportion of archaeogastropods, both in terms of species composition and in terms of absolute numbers. The lesser proportion of archaeogastropods in the Hawaiian fauna as compared with that of the northern Marianas is consistent with what is known of the larval life history of these gastropods: they tend to lack widely dispersing teleplanic larval stages (Kay, 1984) which may prevent them from reaching the Hawaiian chain from the west. Mesogastropods and neogastropods have teleplanic larvae which are taxonomically widespread and therefore are expected in larger proportion. There are, however, some anomalies in the dispersal pattern: for example, only three of the southern-restricted species—*Hipponix foliaceus*, *Cymatium gemmatum*, and *Mitra cucumerina* —— 14% of the southern-restricted species are also found in Hawaii and only one of the common northern-restricted species (*Usilla fusconigra*) is also known from Hawaii.

Other studies of selectivity of dispersal barriers in the ocean have yielded results similar to those we report here. The barrier between the Line Islands in the west and the offshore islands of the eastern Pacific in the east is unselective with respect to apertural shape and shell size (Vermeij, 1978), but there is a selective diminution of numbers of species with apertural modification between the eastern Pacific islands and the mainland coast of western tropical America (Vermeij, 1978). This latter conclusion, however, rests on a small sample, because most of the Indo-west Pacific elements which extend as far east as the offshore islands do not also occur on the mainland (see also Emerson, 1978; Zinsmeister and Emerson, 1979). The selectivity of the Suez Canal as a barrier remains a matter of dispute, but Vermeij's (1978) analysis suggests that there is no strong reduction of any one architectural group of species between the Red Sea and the Mediterranean through the Canal. On the other hand, upper shore species have perhaps been less prone to migration through the Suez Canal from the Red Sea to the Mediterranean than have lower shore species (Safriel and Lipkin, 1975; Vermeij, 1978).

The biogeographical distinctiveness of the gastropods of the upper shore in the northern Marianas recalls the upper shore endemism in the Hawaiian Islands, although endemism per se is not pronounced in the northern Marianas. Similar situations have been reported in the southern tropical Atlantic, western Indian Ocean, and Red Sea (Vermeij, 1972, 1978). The data from the present study suggest that poor dispersability and effective adaptation to locally distinctive environments contribute to the endemism of the high intertidal biota.

Finally, we wish to emphasize that, although faunal surveys have often been maligned as being superficial descriptive studies, they are essential for the understanding of biogeographical affinities, selectivity of barriers, and patterns of diversity. We believe that a comparison of the tropical East Asian mainland biota with that of the northern Marianas will shed further light on the nature of the open-ocean dispersal barrier.

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APPENDIX 1

List of shelled molluscs from the Northern Marianas. An asterisk indicates species characteristic of the northern islands but rare or absent on Guam.

	Anatahan	Guguan	Pagan	Asuncion	Maug	Uracas	Other	Remarks
ARCHAEOGASTROPODA								
Haliotis jacnensis Reeve			×					
**H. ovina* Gmelin		×	×					
**H. planata* Sowerby	×	×	×		×		Agrihan (USNMNH)	
**H. varia varia* Linné		×	×		×		Agrihan	Intertidal
Emarginula dilecta A. Adams		×	×		×		Agrihan	Also in Hawaii
Emarginula sp.		×		×	×			
Scutus unguis (Linné)			×					
Diodora granifera (Pease)		×	×	×	×			Also in Hawaii
Patella flexuosa Quoy and Gaimard	×	×	×	×	×			Intertidal
**Cellana toreuma* (Reeve)	×	×	×	×	×	×		Intertidal
**Notoacmea* cf. *N. shrenki* (Lishke)	×	×	×	×	×		Alamagan	Intertidal
*Acmaeidae sp. A.		×	×	×		×		Intertidal; high conic, radially ribbed, central apex
*Acmaeidae sp. B.	×		×					Intertidal, low-conic, smooth, more or less central apex
Scissurella coronata Watson			×		×			Also in Hawaii
S. cf. *S. pseudoaequatoria* Kay		×	×	×	×			Also in Hawaii

Appendix. (continued)

	Anatahan	Guguan	Pagan	Asuncion	Maug	Uracas	Other	Remarks
S. cf. *S. carinata* Watson					×			
Pseudostomatella sp.			×		×			
**Stomatella planulata* Lamarck	×					×		Intertidal
S. cf. *S. auricula* Lamarck		×	×					
Trochus intextus Kiener			×	×	×			Also in Hawaii
T. maculatus Linné		×	×					
T. ochroleucus Gmelin	×	×	×					
T. pyramis (Born)			×					
Danilia cf. *D. eucheliformis* Nomura and Hatai			×					
Clanculus atropurpureus (Gould)		×	×					
C. clanguloides (Wood)			×	×				Also in Hawaii but extremely rare
Monilea philippiana (Dunker)			×					
Gibbula marmorea (Pease)		×	×	×				Also in Hawaii
Euchelus cf. *E. foveolata* (A. Adams)		×			×			
E. pauperculus (Lischke)		×	×		×			
Synaptocochlea concinna (Gould)		×	×	×	×			Also in Hawaii
Trochidae sp.			×					
Leptothyra cf. *L. inepta* (Gould)			×					
L. cf. *L. maculosa* (Pease)		×	×		×			
Leptothyra sp.					×			

Phasianella solida (Born)			×					
Tricolia variabilis (Pease)		×	×		×			Also in Hawaii
Astraea rhodostoma (Lamarck)		×	×		×			
Turbo argyrostomus Linné	×		×	×	×		Sarigan Alamagan Agrihan	
T. petholatus Linné		×	×		×			
T. setosus Gmelin	×	×	×	×	×		Agrihan	
NERITACEA								
Nerita albicilla Linné			×					Intertidal; also in Hawaii
N. guamensis Quoy and Gaimard	×						Sarigan	Intertidal; dark form only
N. insculpta Recluz			×					Intertidal
N. maxima Gmelin			×					Intertidal
N. plicata Linné		×	×	×	×		Sarigan Alamagan	Intertidal; also in Hawaii but rare except in the Northwest Islands
N. polita Linné			×					Intertidal; also in Hawaii
Puperita bensoni (Recluz)			×					
Neritopsis radula (Linné)			×		×			Also in Hawaii
MESOGASTROPODA								
Littorina coccinea (Gmelin)	×		×				Sarigan	Intertidal; also in Hawaii but rare
L. pintado Wood	×	×	×	×	×	×	Sarigan Agrihan (Rosewater 1970)	Intertidal; also in Hawaii

Appendix. (continued)

	Anatahan	Guguan	Pagan	Asuncion	Maug	Uracas	Other	Remarks
L. undulata Gray			×					Intertidal; also in Hawaii but rare
Nodilittorina millegrana (Philippi)			×					Intertidal
**N. pyramidalis* (Quoy and Gaimard)			×	×	×	×		Intertidal
**N. quadricincta feejeensis* (Reeve)	×	×	×	×	×			Intertidal; see Rosewater and Kadolsky 1981 for nomenclature
Rissoina ambigua (Gould)		×	×	×				Also in Hawaii
R. miltozona Tomlin		×	×	×	×			Also in Hawaii
R. turricula Pease		×	×	×	×			Also in Hawaii
Schwartziella gracilis (Pease)		×						Also in Hawaii
Sansonia sp.		×						
Parashiela beetsi Ladd			×					Also in Hawaii
Pyramidelloides suta (Pilsbry)		×						Also in Hawaii
Zebina imbricata (Gould)					×			Also in Hawaii
Z. tridentata (Michaud)		×	×		×			Also in Hawaii
Brookula cf. *B. iki* Kay		×						Also in Hawaii
Leucorhynchia cf. *L. crossei* (Tyron)					×			
Liotina loculosa (Gould)					×			
Vanikoro acuta (Recluz)			×					Also in Hawaii
V. cancellata (Lamarck)			×					Also in Hawaii
V. distans (Recluz)		×						
Sabia conica (Schumacher)	×	×	×	×	× (USNMNH)		Agrihan	Also in Hawaii

**Planaxis niger* (Quoy and Gaimard)		×	×	×	×	Sarigan Alamagan	Intertidal
P. zonatus A. Adams	×	×	×	×	×	Alamagan	Intertidal
Lopohocochlias minutissimus (Pilsbry)			×	×			Also in Hawaii
Omalogyra japonica (Habe)		×		×			Also in Hawaii
Cyclostremiscus emeryi (Ladd)		×	×	×	×		Also in Hawaii
Orbitestella regina Kay		×		×	×		Also in Hawaii
Caecum arcuatum de Folin		×		×	×		Also in Hawaii
C. oahuense (Pilsbry)		×			×		Also in Hawaii
C. sepimentum de Folin		×	×	×			Also in Hawaii
C. cf. *C. glabellum* A. Adams					×		Also in Hawaii
Modulus tectum (Gmelin)					×		Also in Hawaii
Bittium zebrum (Kiener)		×	×	×	×		Also in Hawaii
B. parcum (Gould)		×	×	×	×		Also in Hawaii
Serpulorbis variabilis Hadfield and Kay			×	×	×		Intertidal; also in Hawaii
Cerithium atromarginatum Dautzenberg and Bouge			×				Also in Hawaii
C. columna Sowerby			×				Also in Hawaii
C. interstriatum Sowerby			×		×		Also in Hawaii
C. egenum Gould		×	×	×	×	Alamagan Agrihan	Also in hawaii
C. mutatum Sowerby	×	×	×		×	Alamagan Agrihan	Also in Hawaii
C. nesioticum Pilsbry and Vanatta		×	×		×		Also in Hawaii
C. nodulosum Bruguière					× (USNMNH)		
C. cf. *C. rubus* Deshayes						Agrihan (USNMNH)	See Rehder (1980) for discussion of this species

Appendix. (continued)

	Anatahan	Guguan	Pagan	Asuncion	Maug	Uracas	Other	Remarks
Rhinoclavis aspera (Linné)	×							
R. fasciata (Bruguière)	×	×	×					Also in Hawaii
R. sinensis (Gmelin)	×		×	×			Sarigan	Large form only; also in Hawaii
Cerithidium perparvulum (Watson)			×	×	×			Also in Hawaii
Cerithidium sp.			×	×				
Diala flammea (Pease)	×							
Finella pupoides A. Adams			×	×	×			Also in Hawaii
Scaliola sp.					×			Also in Hawaii
Dialidae cf. *Alaba* sp.					×			
Strombus dentatus Linné	×							
S. microurceus Kira			×				Agrihan (Abbott 1960)	
S. mutabilis Swainson			×					
S. plicatus pulchellus Reeve			× (Abbott 1960)					
Lambis chiragra chiragra (Linné)				×				
L. truncata sebae (Kiener)			×		×			
Terebellum terebellum (Linné)			×					
Polinices melanostomus (Gmelin)						× (USNMNH)		Also in Hawaii
Naticidae sp.	×							
Lachryma sulcifera (Sowerby)		×	×					

Cypraea caputserpentis Linné	×	×	×	×	×	×	Sarigan Alamagan, Agrihan	Also in Hawaii
C. carneola Linné		×	×		×		Agrihan	Also in Hawaii
C. depressa Gray			×					
C. erosa Linné		×	×		× (USNMNH)			Extremely rare in Hawaii
C. fimbriata Gmelin			×					Also in Hawaii
C. globulus Linné			×		×			Also in Hawaii
C. helvola Linné	×		×	×	×			Also in Hawaii
C. isabella Linné	×	×	×		×	×	Sarigan	Also in Hawaii
C. lynx Linné			×		× (USNMNH)		Alamagan	Extremely rare in Hawaii
C. maculifera Schilder		×	×		×	×		Also in Hawaii
C. mauritiana Linné		×	×		× (USNMNH)		Alamagan Agrihan (USNMNH)	Also in Hawaii
C. moneta Linné	×		×	×	×		Alamagan	Also in Hawaii
C. poraria Linné	×	×	×		×	×	Alamagan Agrihan Sarigan (USNMNH)	Also in Hawaii
C. talpa Linné			×					Also in Hawaii
C. testudinaria Linné			×					
C. teres Gmelin		×						Also in Hawaii
C. vitellus Linné			×					Also in Hawaii
Cassis cornuta Linné			×		×			Also in Hawaii
Casmaria ponderosa (Gmelin)			×					
Cymatium hepaticum (Roding)			×					Also in Hawaii
C. muricinum (Roding)					× (USNMNH)			Also in Hawaii
C. nicobaricum (Roding)							Agrihan (USNMNH)	Also in Hawaii

Appendix. (continued)

	Anatahan	Guguan	Pagan	Asuncion	Maug	Uracas	Other	Remarks
C. pileare (Linné)			×				Agrihan (USNMNH)	Also in Hawaii
Bursa bufonia (Gmelin)	×		×					Also in Hawaii
B. granularis (Roding)		×	×					Also in Hawaii
NEOGASTROPODA								
Muricodrupa funiculus (Wood)			×					Also in Hawaii
Thais armigera (Link)	×	×	×		×			Intertidal; also in Hawaii
T. tuberosa (Roding)		×	×					
T. intermedia (Kiener)	×	×	×		× (USNMNH)			Intertidal; also in Hawaii
Purpura persica (Linné)	×	×	×		×	×		Intertidal
Morula biconica (Blainville)		×	×	×				
M. granulata (Duclos)	×	×	×	×				Intertidal; also in Hawaii
M. spinosa (H. & A. Adams)	×							Also in Hawaii
M. uva (Roding)	×	×	×	×	×		Agrihan	Intertidal; also in Hawaii
Drupella elata (Blainville)			×		× (USNMNH)			Also in Hawaii
D. ochrostoma (Blainville)			×				Agrihan (USNMNH)	Also in Hawaii
Drupa arachnoides (Lamarck)	×		×	×	×		Sarigan	Also in Hawaii; we regard this as a distinct species although it is not recognized as

							such by Emerson and Cernohorsky (1973)
D. clathrata clathrata (Lamarck)		×	×		×		Maug record that of Emerson and Cernohorsky (1973)
D. grossularia (Roding)		×	×			Agrihan	Also in Hawaii but almost entirely restricted to the Northwest Hawaiian Islands
D. morum morum (Roding)	×	×	×		×	Alamagan Agrihan	Intertidal; also in Hawaii
D. ricinus (Linné)	×	×	×	×	×		Intertidal; also in Hawaii
D. rubusidaeus (Roding)	×		×	×	×		Intertidal; also in Hawaii
Nassa serta (Bruguière)			×				Also in Hawaii
Maculotriton bracteata (Hinds)			×		×		Also in Hawaii
**Usilla fusconigra* (Pease)	×		×				Intertidal; also in Hawaii
Chicoreus brunneus (Link)					× (USNMNH)		
Coralliophila violacea (Kiener)	×		×				Also in Hawaii
Quoyula monodonta (Blainville)			×			Agrihan	Also in Hawaii
Caducifer decapitata fuscomaculata (Pease)			×				Also in Hawaii
C. iostomus (Gray in Griffiths and Pidgin)			×				Also in Hawaii

Appendix. (continued)

	Anatahan	Guguan	Pagan	Asuncion	Maug	Uracas	Other	Remarks
Pisania ignea (Gmelin)		×						Also in Hawaii
Cantharus fumosus (Dillwyn)					× (USNMNH)			
C. undosus (Linné)	×	×	×		× (USNMNH)			
Nassarius gaudiosus (Hinds)			×				Agrihan	Also in Hawaii
N. papillosus (Linné)			×					Also in Hawaii
N. pauperus (Gould)		×	×	×				Also in Hawaii
Euplica deshayesi (Crosse)			×					
E. turturina (Lamarck)			×					Also in Hawaii but rare in the windward islands
E. varians (Sowerby)			×					Also in Hawaii
Pyrene obtusa (Sowerby)				×	× (USNMNH)			
Oliva annulata Gmelin	×							
Seminella virginea (Gould)				×	×			Also in Hawaii
Seminella sp.				×				
Vasum ceramicum (Linné)	×	×	×	×	×	×	Sarigan Alamagan	
V. turbinellus (Linné)					× (USNMNH)			
Latirus barclayi (Reeve)	×	×	×	×	× (USNMNH)	×	Agrihan	
L. nodatus (Gmelin)	×		×			× (USNMNH)	Almagan Agrihan (USNMNH)	Also in Hawaii
L. noumeensis (Crosse)			×					

Peristernia nassatula (Lamarck)	×		×	×	×	Alamagan Agrihan	
Mitra chrysostoma Broderip			×		×		
M. imperialis (Roding)					×		Maug record that of Cernohorsky (1976)
M. stictica (Link)			×				Also in Hawaii
Strigatella fastigium (Reeve)		×	×		×		Also in Hawaii
S. litterata (Linné)	×	×	×				Intertidal; also in Hawaii
S. paupercula (Linné)		×	×				
S. pellisserpentis (Reeve)			×	×			Also in Hawaii
**Strigatella* sp.	×	×	×				
Nebularia aurora floridula (Sowerby)						Sarigan	
N. ferruginea Lamarck		×	×			Agrihan (USNMNH)	Also in Hawaii
N. chrysalis (Reeve)					× (USNMNH)		
Costellaria crocata (Lamarck)			×				Also in Hawaii
C. coronatum (Helbling)			×				
C. unifascialis (Lamarck)						Alamagan	Also in Hawaii
C. pacificum (Reeve)			×				
**Pusia* sp.			×				
Pusia amabilis (Reeve)	×		×				
P. cancellarioides (Anton)						Agrihan	Also in Hawaii
P. consanguinea (Reeve)			×				Also in Hawaii
P. lauta (Reeve)			×				Also in Hawaii

Appendix. (continued)

	Anatahan	Guguan	Pagan	Asuncion	Maug	Uracas	Other	Remarks
P. microzonias (Lamarck)	×		×					Also in Hawaii
P. patriarchalis (Gmelin)		×	×				Agrihan (USNMNH)	Also in Hawaii
P. speciosa (Reeve)			×					
Imbricaria olivaeformis (Swainson)			×					Also in Hawaii
I. punctata (Swainson)			×				Sarigan	Also in Hawaii
Terebra affinis Gray			×					Also in Hawaii
T. crenulata (Linné)		×	×					Also in Hawaii
T. dimidiata (Linné)			×		× (USNMNH)			Also in Hawaii
T. felina (Dillwyn)				×				Also in Hawaii
T. laevigata (Gray)				×				
Hastula solida (Deshayes)	×							Also in Hawaii
Hastula strigillata (Linné)			×					Also in Hawaii
Lienardia sp.			×					
L. cf. *L. mighelsi* Iredale and Tomlin			×		×			
Carinapex minutissima (Garrett)			×					Also in Hawaii
Macteola segesta (Chenu)			×					Also in Hawaii
Iredalea sp.			×					
Tritonoturris sp.		×						
**Conus aulicus* Linné			×					
C. balteatus Sowerby	×						Alamagan Agrihan	
C. bandanus Hwass	×		×				Alamagan	

*C. *canonicus* Roding			×				Agrihan (USNMNH)	
C. *capitaneus* Linné							Alamagan	Also in Hawaii
C. *catus* Hwass	×		×				Agrihan	Also in Hawaii
C. *chaldaeus* (Roding)			×		× (USNMNH)			Also in Hawaii
C. *coronatus* (Hwass)			×		× (USNMNH)			Also in Hawaii
C. *distans* Hwass		×					Agrihan	Also in Hawaii
C. *ebraeus* Linné	×		×					Also in Hawaii
C. *flavidus* Lamarck	×	×	×	×	×		Agrihan	Also in Hawaii
C. *frigidus* Reeve			×				Agrihan	
C. *fulgetrum* Sowerby			×					
C. *generalis* Linné			×				Agrihan (USNMNH)	
C. *geographus* Linné			×					
C. *imperialis* Linné					×		Agrihan	Also in Hawaii
C. *litoglyphus* Hwass	×	×	×				Alamagan	Also in Hawaii
C. *lividus* Hwass	×	×	×				Alamagan	Also in Hawaii
C. *magnificus* Reeve			×		×			
C. *marmoreus* Linné	×							Also in Hawaii
C. *miles* Hwass		×	×	×	×	×	Alamagan Agrihan	Also in Hawaii
C. *miliaris* Hwass	×	×	×	×	×		Alamagan Agrihan	Also in Hawaii
C. *moreleti* Crosse	×	×	×	×				Also in Hawaii
C. *musicus* Hwass			×				Agrihan	
C. *nanus* Sowerby	×	×	×	×	×	×	Sarigan Agrihan	
C. *obscurus* Sowerby			×					Also in Hawaii
C. *pertusus* Hwass		×						Also in Hawaii
C. *pulicarius* Hwass	×	×	×	×	×			Also in Hawaii
C. *rattus* Hwass		×	×	×	×		Sarigan Alamagan Agrihan	Also in Hawaii

Appendix. (continued)

	Anatahan	Guguan	Pagan	Asuncion	Maug	Uracas	Other	Remarks
C. sanguinolentus Quoy and Gaimard		×	×					
C. sponsalis Hwass	×	×	×	×			Sarigan Agrihan	Also in Hawaii
C. striatus Linné			×				Agrihan (USNMNH)	Also in Hawaii
C. tessulatus Born							Agrihan (USNMNH)	
C. tulipa Linné			×		×			
C. varius Linné			×					
C. virgo Linné		×						
EUTHYNEURA								
Micromelo guamensis (Quoy and Gaimard)			×					Also in Hawaii
Smaragdinella calyculata (Broderip and Sowerby)	×	×	×	×				Intertidal; also in Hawaii
Haminoea cymbalum (Quoy and Gaimard)	×	×		×				Also in Hawaii
Haminoea sp.		×	×		×			
Acteocina hawaiensis Pilsbry		×			×			Also in Hawaii
Acteocina sp.					×			
Cylichna sp.		×						
Retusa sp.		×		×				
Atys sp.		×						
Siphonaria cf. *S. guamensis* (Quoy and Gaimard)			×					Intertidal

**S. sirius* Pilsbry	×	×	×				Intertidal
Williamia radiata (Pease)			×	×			Also in Hawaii
Melampus castaneus (Muhlfeld)	×		×	×		Sarigan	Also in Hawaii; spray zone
M. flavus (Gmelin)			×				Spray zone
Miralda cf. *M. scopulorum* Watson		×					
Pyramidellidae sp. 1		×					
Pyramidellidae sp. 2		×		×	×		
Pyramidellidae sp. 3		×	×		×		
Julia exquisita Gould		×		×			Also in Hawaii
POLYPLACOPHORA							
Acanthopleura gemmata (Blainville)	×		×		×. (USNMNH)		Intertidal
Polyplacophora sp.			×				
BIVALVIA							
Arca avellana Lamarck			×		×		
A. ventricosa Lamarck	×		×	×	×		Also in Hawaii
Acar divaricata (Sowerby)			×		×		Also in Hawaii
Barbatia descussata (Sowerby)			×		×		Also in Hawaii
B. amygdalumtostum Roding			×				
B. tenella Reeve			×				Also in Hawaii
Modiolus auriculatus (Krauss)			×				
Septifer excisus (Wigmann)		×	×				

Appendix. (continued)

	Anatahan	Guguan	Pagan	Asuncion	Maug	Uracas	Other	Remarks
Chlamys coruscans coruscans (Hinds)			×					In Hawaii as *C. c. hawaiensis*
C. squamosa (Gmelin)		×	×					
Spondylus sp.		×			×			
Lima annulata (Lamarck)			×					
L. lima (Linné)			×					
**Glycymeris* sp.			×					
Pinctada margaritifera (Linné)		×	×					Also in Hawaii
Pinctada sp.			×					
Isognomon perna (Linné)			×					Also in Hawaii
I. incisum (Conrad)			×					Also in Hawaii
Pycnodonte numisma (Lamarck)					× (USNMNH)			
Cardita variegata (Brugiuère)					×			
Trapezium oblongum (Linné)			×		×			Also in Hawaii
Fimbria fimbriata (Linné)					×			Maug record from Nicol (1950)
Fimbria sp.			×					
Chama iostoma (Conrad)		×	×		×			Also in Hawaii
Chama sp.		×					Agrihan	
Tridacna maxima Roding			×		×		Sarigan	
T. squamosa Lamarck	×				×			
Lioconcha hieroglyphica (Conrad)					×			Also in Hawaii
Gafrarium pectinatum (Linné)			×					

Periglypta reticulata (Linné)		×			Also in Hawaii
Nesobornia bartschi Chavan		×			Also in Hawaii
Quidnipagus palatam Iredale		×			Also in Hawaii
Pinguitellina robusta Hanley		×			Also in Hawaii
Tellina crucigera Lamarck		×			Also in Hawaii
Tellina sp.				×	
Ervilia sandwichensis (Smith)	×			×	Also in Hawaii
Ctena bella (Conrad)	×			×	Also in Hawaii
Limopsis sp.	×				
Carditella cf. *C. hawaiensis* Dall, Bartsch and Rehder			×		

APPENDIX 2

Molluscs common in the southern Marianas but unknown from the northern Marianas (only species living on hard bottom are included)

Species	Intertidal	Reef
Cellana radiata orientalis (Pilsbry)	+	
Patelloida sp.	+	
Trochus niloticus (Linné)		+
Echininus viviparus Rosewater	+	
Planaxis sulcatus (Born)	+	
Alvinia crystallina (Garrett)		+
Cerithium sejunctum Iredale		+
C. zonatum Wood		+
Clypeomorus alveolus (Hombron and Jacquinot)	+	
C. bifasciatus (Sowerby)	+	
C. moniliferus (Kiener)	+	
Hipponix foliaceus (Quoy and Gaimard)		+
Cypraea annulus Linne		+
Cymatium gemmatum (Reeve)		+
Thais aculeata Deshayes and Milne Edwards		+
Morula fiscella (Gmelin)		+
M. nodicostata (Pease)		+
M. squamosa (Pease)	+	
Morula sp.		+
Muricodrupa fenestrata (Wood)		+
Nebularia cucumerina (Lamarck)		+
Strigatella decurtata (Reeve)		+

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