The Littoral Marine Molluscs of Fanning Island[1]

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WHEREAS there is a wealth of taxonomic literature on the marine molluscs of the Indo-West-Pacific and a surfeit of speculation on the characteristics and relationships of insular faunas in the region, the ecological aspect of the zoogeography has been largely neglected. An expedition to Fanning Island in the Line Islands in January 1970 gave opportunity for determining the commonly occurring reef and lagoon molluscs of this Pacific atoll, and also for conducting preliminary surveys on their general ecology, especially of the dominants, and their local distribution. Information so obtained is used to describe the composition of the Fanning Island marine molluscan fauna and its relationships with those of other Pacific islands. A list of species from the Line Islands (Table 1) compiled from collections in the Bernice P. Bishop Museum, Honolulu, Hawaii, made during the Whippoorwill Expedition in 1924 is included for comparative purposes.

Fanning Island lies midway in the string of shoals and atolls extending from 8° N latitude to 12° S latitude which constitute the Line Islands. Above the equator these islands form the most southerly and easterly fringe of the faunal area termed by Ekman (1953) the "Central Pacific." The major islands in the Lines (Washington, Palmyra, Fanning, Christmas) are about 1,000 miles south, southeast, and northeast of Hawaii, Johnston Island, and the Phoenix Islands, respectively; they are 1,200 miles northwest of Tahiti and 1,500 miles northwest of the Tuamotus. An outlier, Jarvis Island, is 400 miles southwest of Fanning; other outliers such as Malden, Starbuck, and Flint are below the equator.

METHODS

A variety of sampling methods, adapted to tides, wave action, topography, and available time, was used in the study. Four seaward reef stations were sampled by transect, with quadrat counts from a 45-cm ring or timed counts made at meter intervals from the shore toward the seaward edge of the reef. The lagoon molluscs were surveyed by sampling patch reefs and analyzing sediments and beachdrift. Additional records were obtained from various collections made by divers engaged primarily in studies of fish populations.

SUPRATIDAL AND HIGH TIDAL MOLLUSCS

The supratidal and high tidal regions (littorinid zone of Stephenson and Stephenson, 1949; littoral fringe and upper eulittoral of Morton and Challis, 1969) of seaward and lagoon shores were characterized at Fanning as everywhere else by littorines and nerites. Three species of *Littorina* occurred, although only *L. coccinea* was abundant. This species was found on shingle landward of the seaward reef flat, on beachrock and raised limestone along lagoon shores, and on trees overhanging the water. *L. scabra* was much less common; specimens were found on the branches of *Messerschmidia* (*Tournefortia*) along the lagoon shore and on rocks at Napu Naiaroa (Fig. 1). Fewer than six specimens of *Littorina undulata* were recorded, from two areas only, along a channel between the berm and the island at Vai Tepu (Fig. 1, *S–D*) and on shingle at Cartwright Point (Fig. 1, *L–A*).

Two marine pulmonates and two prosobranchs were also found in the littorinid zone, *Melampus luteus*, *Melampus* sp., *Truncatella* sp., and *Assiminea nitida*. These gastropods occurred under loose rubble and deep in shingle along both seaward and lagoon shores. *Assiminea* was also found in the estuarine flat at Napu Naiaroa (Guinther, Pacific Science, this issue).

Nerita plicata, the widespread nerite characteristic of most tropical shorelines from east Africa to the east Pacific barrier (Ekman, 1953),

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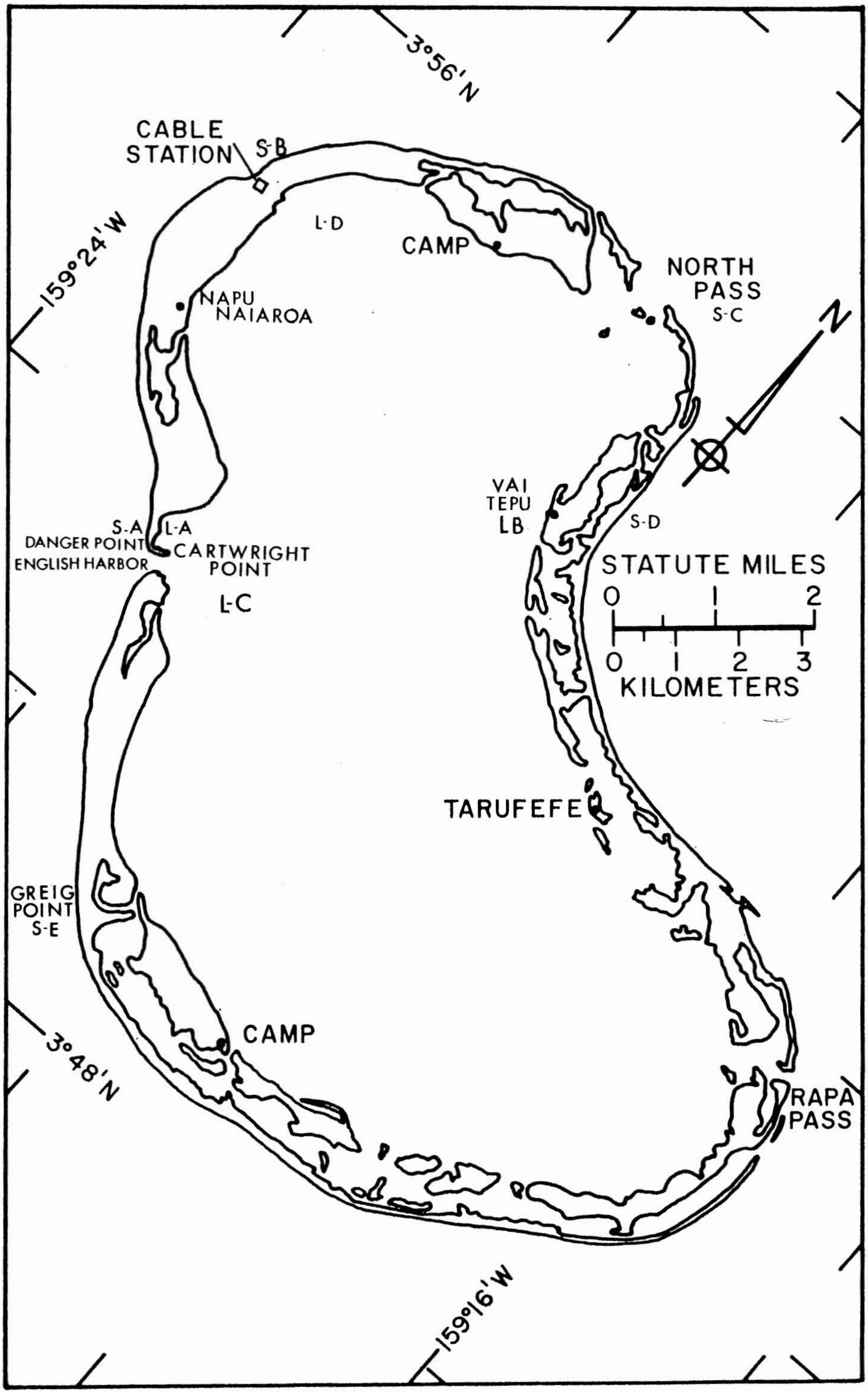

FIG. 1. Map of Fanning Island showing the areas collected in January 1970.

was the single dominant nerite seaward of the littorines. It was found in great abundance wherever there was shingle or other hard substrate. Some animals ranged as high as the littorines, but the major portion of the population remained at mean low water, with the snails moving landward and seaward with the tides. Most of the nerites were found along the seaward shoreline; they were perhaps less common along lagoon shores because of the absence of suitable substrate.

MOLLUSCS OF THE SEAWARD REEFS

REEF TOPOGRAPHY: The seaward reef platform was a narrow (about 30 m) flat backed by a shingle berm which encircled the atoll, broken only at the three passes (Fig. 1).

At Danger Point and North Pass (Fig. 1, *S–A, S–C*), the two pass areas sampled, three types of habitat could be conveniently distinguished: moat, shingle, and beachrock. Relatively large moats or pools were separated from the seaward reef flat in both areas by an offshore ridge of shingle which rose to a height of about 2 m (Fig. 2). The moats (about 125 m by 225 m and larger) varied in depth from a few cm to more than a m depending on tide and wave action. Temperatures were on the order of 27.5° C in January (De Wreede, personal communication); Bakus (1964) reported 31.5° C at Danger Point in August. Salinities were approximately 35 ‰ (De Wreede, personal communication). The moats contained a variety of habitats: a rich assemblage of corals such as *Porites* and *Pocillopora,* dead coral heads and rubble, patches of sand, and some reef limestone with varying algal cover. Seaward of the moats the offshore ridge sloped as shingle over the reef flat for more than 20 m. The shingle was smooth and slippery with *Centroceros* and other red algae. At Danger Point the shingle was replaced at the north end of the moats by a relatively smooth substrate of beachrock, and emergent patches of beachrock were scattered along the shoreward edge of the moats. The latter patches were somewhat protected from wave action by the offshore wall; they were covered thinly by algae and sand. At North Pass similar islands of beachrock were scattered throughout the shallow, sandy pass area, some of the patches being more pitted and rubble-strewn than others. Both shingle and beachrock were alternately exposed and inundated by the tides.

The reef flats were narrow, backed at the shoreward extremity by beachrock and/or shingle and broken 20 to 30 m seaward by emergent coral boulders separated by deep, wide surge channels (Fig. 3). Physically similar, the reefs differed in appearance at each of the stations sampled. At Greig Point (Fig. 1, *S–E*) the reef flat was covered by a thick mat of the red coralline alga *Jania* which formed tufts up to 3 cm in height in the shoreward portions of the flat. The alga binds considerable amounts of sand among its fronds and the mat was estimated as consisting of from 50 to 60 percent sand. At Vai Tepu (Fig. 1, *S–D*) the reef flat was littered by shingle festooned with green

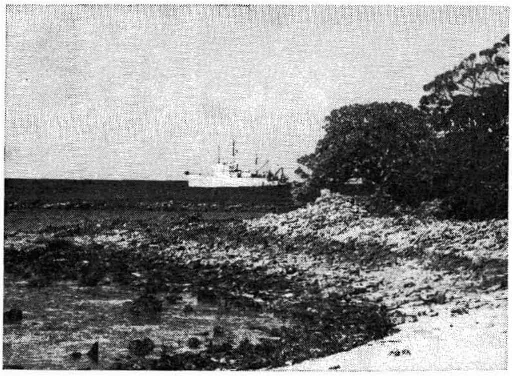

FIG. 2. Moats at Danger Point with shingle and beachrock backshore and the offshore ridge.

FIG. 3. The reef flat at Greig Point. Photograph by E. D. Stroup.

algae such as *Caulerpa* and *Ulva.* At Teuru Mangaru (Fig. 1, *S–B*) the reef flat was surfaced with an algal-sand mat tufted with *Turbinaria* and pitted by depressions, some of which contained small heads of *Porites.* All three reefs were generally submerged except at extreme low tides and all were subject to strong surf and surge.

MOLLUSCAN FAUNA: The macromolluscan fauna of the seaward reefs consisted of large percentages of the thaisids *Drupa, Morula,* and *Maculotriton,* and lesser numbers of *Vasum, Patella, Cypraea,* and *Conus.*

The moats in the pass areas supported the most diverse molluscan fauna. The most abundant species at Danger Point, *Morula uva, Drupina grossularia, Cypraea moneta, Turbo argyrostomus, Conus sponsalis, Euplica turturina,* and *Latirus amplustris,* made up more than 60 percent of the samples (Fig. 4). The moat-dwelling gastropods reflect the variety of habitats available in the pools. The dominants were principally found on beachrock and large pieces of rubble, and among the less abundant ones, some are associated with living coral (*Coralliophila* and *Quoyula*) and others are sand-dwellers (*Imbricaria* spp. and *Terebra* spp.). The gastropod : bivalve ratio (based on species) was 97 : 3. In terms of food habits, 34 percent of the prosobranch species were algal feeders, 51 percent active predators, 8 percent scavengers, and 7 percent faunal grazers.[3] Two of the bivalves (*Modiolus metcalfei* and *Tridacna maxima*) were suspension feeders, bysally attached or cemented to the substratum; the third was an erycinid, which moved freely in the rubble.

In addition to the 44 macromolluscan species in the Danger Point moats, 65 species of micromolluscs (those less than 1 cm in length) were recorded from samples of beach drift at the edge of the moats. Although this fauna may have been composed partially of waifs, one or two specimens of most of the species were collected alive in the pools; it is felt that the assemblage gives some indication of the great variety associated with the microhabitats in the moats. The dominant species are shown in Figure 5. The faunal composition of the assemblage was somewhat different from that recorded for the larger species: there was a greater percentage of bivalves in the gastropod : bivalve ratio (86 : 14), and among prosobranch species, 42 percent were algal feeders, 39 percent faunal grazers, and 19 percent active predators.

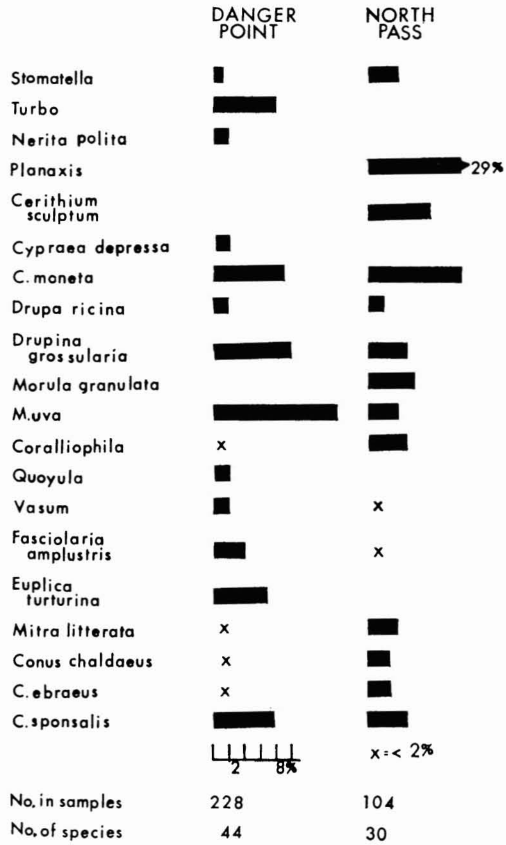

FIG. 4. Assemblages of macromolluscs at Danger Point and North Pass moats. Percentages show relative abundance in total assemblage in this and succeeding figures. Species occurring in monotypic genera at Fanning are cited by genus only.

Shingle supported a lesser number of species than did the moats; 14 species were recorded from Danger Point and 19 from North Pass. The assemblage was dominated by *Maculotriton digitalis, Euplica varians, Engina tuberculosa,* and *Drupa ricina* (Fig. 6); their local distribution at North Pass is shown in Figure 7. The only bivalve found among the gastropods was *Ostrea hanleyana,* which was occasionally ce-

[3] Calculations for feeding habits based on numbers rather than species do not appreciably change the figures.

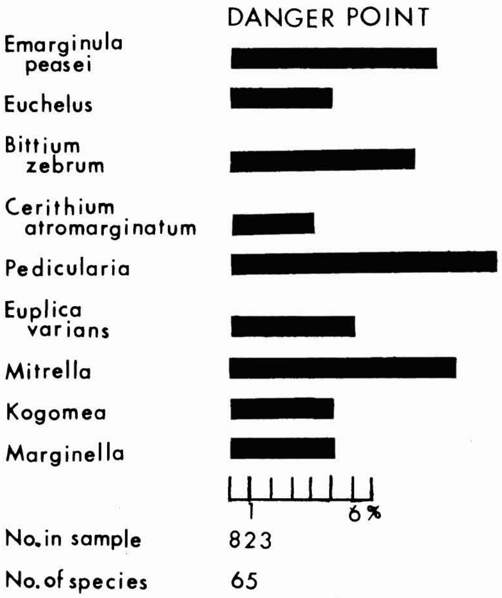

FIG. 5. The assemblage of micromolluscs collected from beachdrift in the Danger Point moats.

mented to the undersurfaces of the shingle. At Danger Point 28 percent of the prosobranch species were algal feeders, 58 percent active predators, 7 percent scavengers, and 7 percent

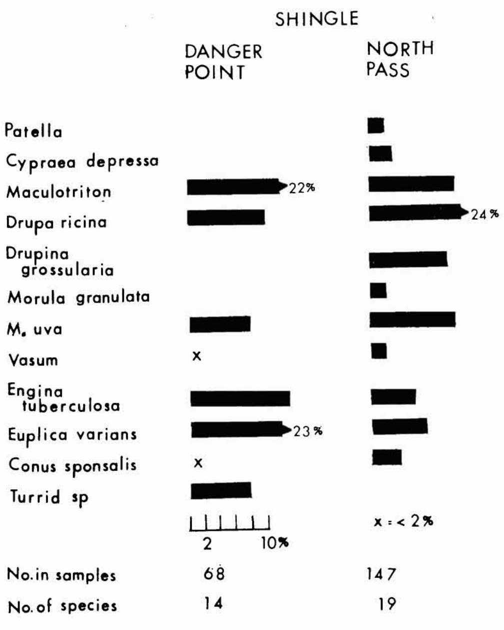

FIG. 6. Assemblages of macromolluscs from shingle at Danger Point and North Pass.

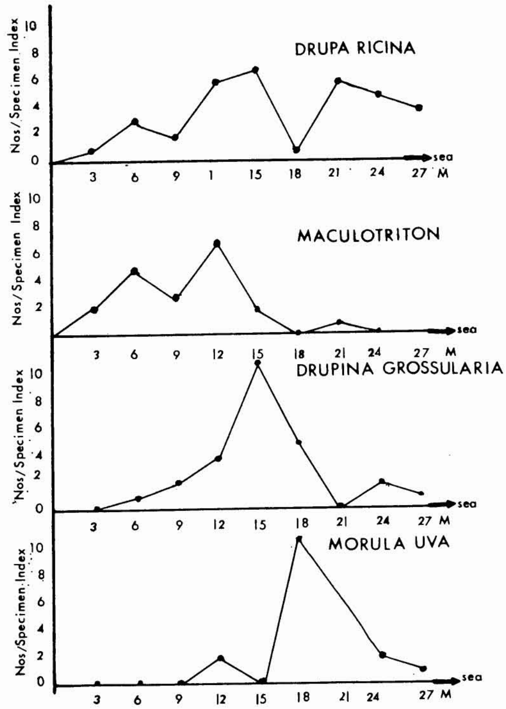

FIG. 7. The distribution of the most abundant species on shingle at North Pass. The specimen index represents three 20-second counts at each meter interval.

faunal grazers. At North Pass 37 percent were algal feeders, 52 percent active predators, and 11 percent scavengers. Most of the molluscs of the shingle were cryptofaunal at least during the day and were found on the undersurfaces.

Beachrock also supported fewer species than did the moats: at Danger Point seven species were recorded on the wave-washed seaward reef flat and five on the protected flats shoreward of the moats (Fig. 8). *Drupa ricina* and *Morula granulata* were dominant on the seaward-facing beachrock, and *Drupina grossularia* and *Vasum armatum* on the protected shoreward beachrock. At North Pass, where the beachrock was more physically varied and protected from the main force of the waves, 21 species were recorded; *Vasum* was again dominant, and *Cypraea moneta* and *Morula uva* were also present (Fig. 8). A few specimens of *Thais aculeata* were noted on backshore beachrock at North Pass but they did not appear in the samples. Of the prosobranch species, 27 percent were algal feed-

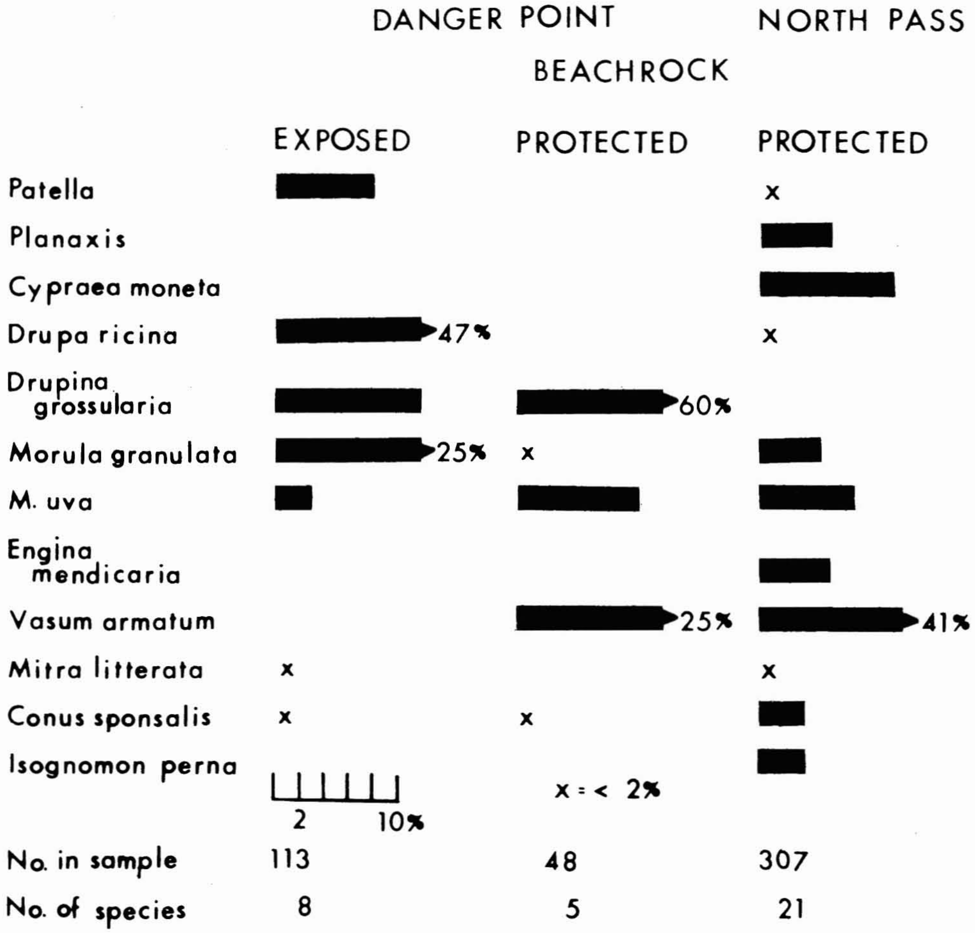

FIG. 8. Assemblages of macromolluscs from beachrock at Danger Point and North Pass.

ers, 66 percent active predators, and 7 percent scavengers.

In faunal composition the two reef flats sampled by transects differed from the habitats of the passes. Seventeen species were recorded from a 20-m transect at Teuru Mangaru (Fig. 1, *S–B*) and 30 from the *Jania*-sand mat transect at Greig Point (Fig. 1, *S–E*). The dominant species at Teuru Mangaru were *Morula uva* and *Drupina grossularia* which formed 56 percent of the samples (Fig. 9); the vermetid gastropod *Serpulorbis* was also conspicuous on the reef flat but densities were not estimated because of surge. At Greig Point *Drupa ricina, D. morum,* and *Patella stellaeformis* formed 62 percent of the samples (Fig. 9). The local distribution of the dominants is shown in Figure 10. No bivalves were recorded in the transects at Greig Point although occasional specimens of *Tridacna maxima* and *Modiolus metcalfei* were found in the area. At Greig Point, 24 percent of the prosobranch species were algal feeders, 66 percent active predators, 7 percent faunal grazers, and 3 percent scavengers; at Teuru Mangaru, 24 percent were algal feeders and 76 percent were active predators.

The reef flat at Vai Tepu (Fig. 1, *S–D*) was not sampled by transect because of surge, but molluscs collected randomly on the reef were similar in species composition to those at Teuru Mangaru and Greig Point, with the exception of a greater number of specimens of *Thais armigera* in the surge channels at this station.

Micromolluscs were found in the algal-sand

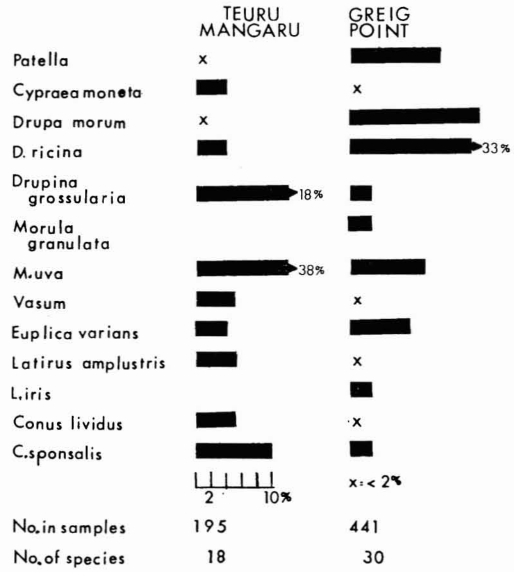

FIG. 9. Assemblages of macromolluscs on the reef flats at Teuru Mangaru and Greig Point.

mat of the reef flats. Thirty-four species were recorded from Teuru Mangaru, 10 from Greig Point, and six from Vai Tepu. *Euplica varians* was the most abundant species at Teuru Mangaru and Vai Tepu, but was second in abundance at Greig Point where minute specimens of the

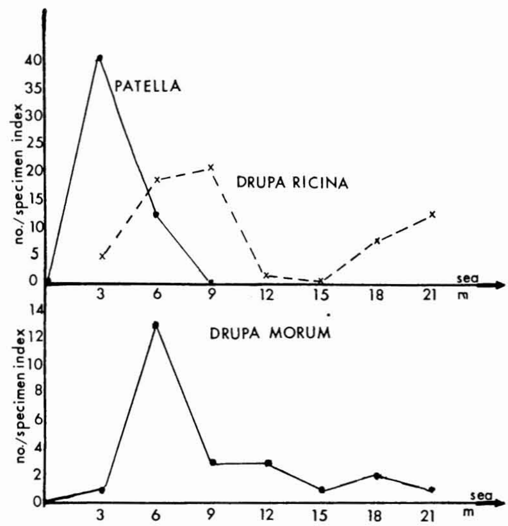

FIG. 10. The distribution of the most abundant species of macromolluscs on the reef flat at Greig Point. The specimen index represents four 20-second counts at each meter interval.

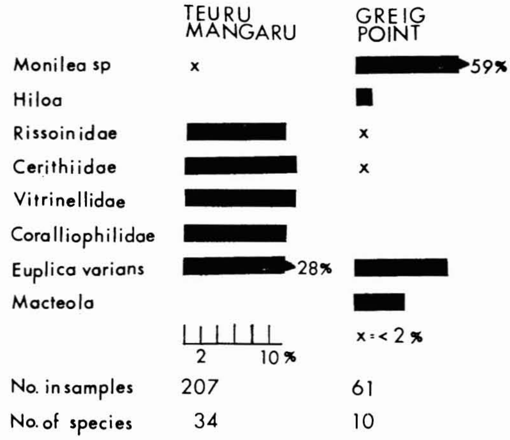

FIG. 11. Assemblages of micromolluscs from the algal-sand mat of the reef flats at Teuru Mangaru and Greig Point.

trochid *Monilea* were dominant (Fig. 11). At Teuru Mangaru algal feeders constituted 61 percent of the prosobranch species, active predators 21 percent, and faunal grazers 18 percent. At Greig Point algal feeders formed 70 percent of the prosobranchs, active predators 10 percent, and faunal grazers 20 percent.

DISCUSSION: Perhaps the most conspicuous feature of the molluscan populations of the seaward reefs was the faunal homogeneity. Of the 20 most abundant species of macromolluscs, 78 percent occurred in more than half the sampling areas. Gastropods were far more numerous than bivalves at all stations. Among food habits of the prosobranchs, active predators were dominant among the macromolluscs at all stations, whereas algal feeders and faunal grazers predominated among the micromolluscs (Fig. 12).

Drupa ricina and *Morula uva* were the most regularly found gastropods in the samples, *Drupa ricina* being somewhat more generally distributed across the reef flats than *Morula uva* (Fig. 10). *Drupa ricina* is a food generalist, feeding on molluscs, barnacles, and worms; *Morula uva* is more a food specialist, eating principally sessile gastropods of the family Vermetidae (Miller, personal communication). *Drupina grossularia* was also a dominant at most of the stations, but it showed a more irregular distribution across the reef flats than did the former two species.

The faunal homogeneity was not perfect, of

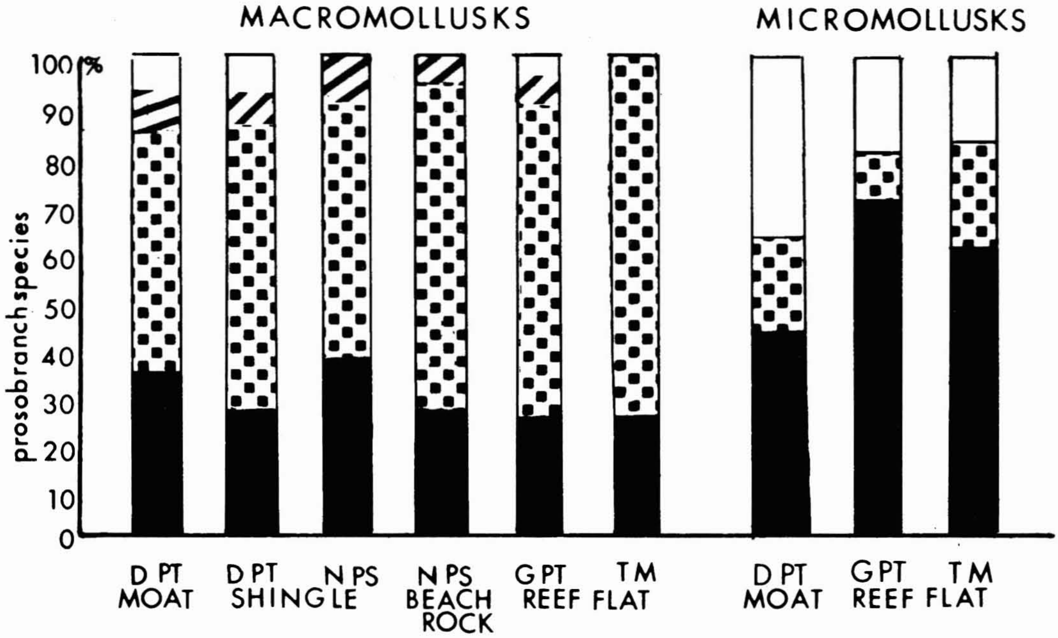

FIG. 12. Summary of the feeding habits of macro- and micro-molluscs on the seaward reefs. Solid black represents algal feeders; dots, active predators; diagonals, scavengers; and white, faunal grazers. D. Pt. = Danger Point; N. Ps. = North Pass; G. Pt. = Greig Point; T. M. = Tearu Mangaru.

course, since a number of local distribution patterns existed. These were principally associated with substrates—the shingle and beachrock of the pass areas and the reef flats—which were alternately exposed and immersed by tidal and wave action. *Drupa morum* was found only on algal-sand mat (on the reef flats rather than on shingle or beachrock), a habit no doubt consistent with its diet of worms and sipunculids (Bernstein, personal communication). *Morula granulata* and *Vasum* occupied principally smooth substrates; the former is a food generalist feeding on other molluscs and tube worms and is found in more exposed situations than the latter. *Maculotriton, Engina tuberculosa,* and *Euplica varians* in concert were characteristic of shingle, although *E. varians* was also abundant in the algal-sand mat of the reef flats. *Engina mendicaria* and *Thais aculeata* lived on beachrock in protected backshore areas but did not overlap in their distribution and were restricted to small areas. *Thais armigera,* which was not recorded in the transects, was found at the outer edge of the reef flats near or in surge channels. *Latirus amplustris* and *L. iris* were at most stations, with the former usually submersed and the latter exposed on shoreward areas of the reef flat.

The diverse fauna of the moats included not only species which forage over shingle, beachrock, and the reef flats (42 percent of the macromolluscs), but forms which are characteristically subtidal, such as *Coralliophila, Columbella tuturina, Terebra,* and *Imbricaria.* The physical structure of the moats formed, in part at least, an essentially subtidal habitat similar to that of subtidal coral reef platforms.

LAGOON MOLLUSCS

The Fanning Lagoon is a shallow basin of approximately 116.55 km^2, with a deep pass at English Harbor. The most active area of coral growth was in the western lagoon near the English Harbor pass, where the reefs were at depths of 10 m. The passes in the southeast (Rapa) and north (North Pass) were not well defined; they were shallow sand flats covered by less than a meter of water. The northern and southern portions of the lagoon were shallow and laced with line and patch reefs. Water temperatures in January were about 27.5° C throughout the lagoon with little vertical change; salinities fluctuated around 35 ‰ (Gordon and Schiesser, Pacific Science, this issue). At least five major molluscan assemblages could be recognized in the lagoon, with little overlap in species among the assemblages.

The lagoon reef flat, with the exception of a small area at Cartwright Point, was composed almost entirely of sand. At Vai Tepu (Fig. 1, *L–A*) the dominant macromollusc was the cerithid *Rhinoclavis asper;* in addition, specimens of *Cerithium breve* occurred, but this species was principally estuarine (Guinther, Pacific Science, this issue). Thirty-five species of micromolluscs were also listed from sediment samples from this station; most of the shells were dead and the habits of these animals, with the exceptions of *Acteocina* (a sand-dweller) and *Hiloa* (which was found on algae), are not known. *Diala flammea, Obtortio pyrrhacme,* and *Hiloa variabilis* constituted 82 percent of the assemblage (Fig. 13). The gastropod : bivalve ratio was 85 : 15; and the prosobranch : opisthobranch ratio (based on species) was 86 : 14.

Collections of dead shells from the shoreline of the reef flat in other areas suggest that additional assemblages occur at various places around the lagoon. These collections included shells of *Pupa, Pyramidella, Ctena divergens,* and various tellinids.

A unique lagoon reef-flat habitat occurred at Cartwright Point near English Harbor where a spit on the lagoon reef paralleled the pass (Fig. 1, *L–A*). The shoreline was made up of coral slabs which extended from 3 to 6 m into the lagoon but which were never more than 0.5 to 1 m in depth.

The living fauna was a mixture of species associated with the seaward reefs, patch reefs of the lagoon, and species which were found nowhere else at Fanning. *Cypraea moneta, Euplica varians, Neritina bensoni, Planaxis lineata,* and *Maculotriton digitalis* formed approximately 70 percent of the assemblage (Fig. 14). Of these, only *Planaxis* was locally distributed, occurring in the shoreward 2 meters of the transects. The gastropod : bivalve ratio was 78 : 22; among the prosobranchs 44 percent were algal feeders and 56 percent active predators. Molluscs which occurred here but were not

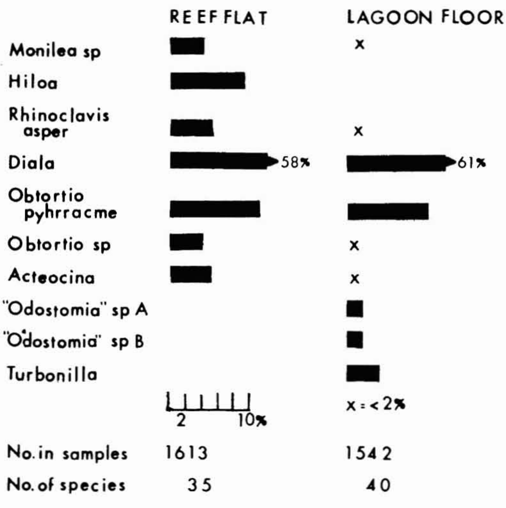

FIG. 13. Assemblages of micromolluscs from the lagoon reef flat (Station *L–A*) and the lagoon floor (Station *L–D*).

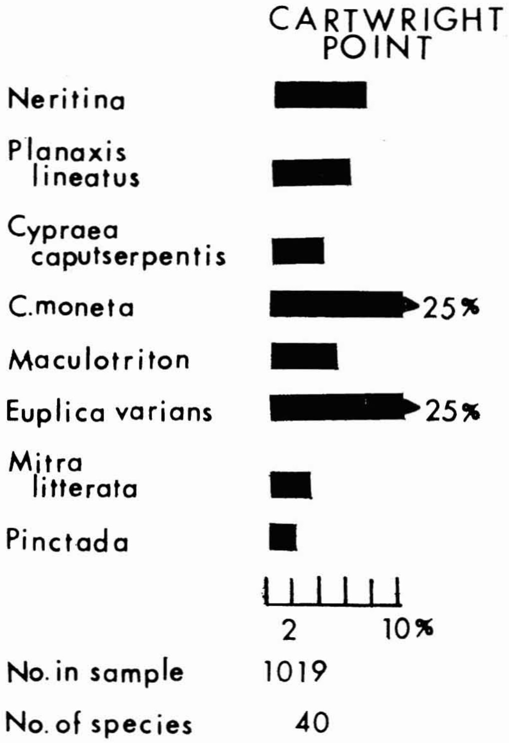

FIG. 14. The assemblage of macromolluscs from Cartwright Point.

found elsewhere include the prosobranchs *Cypraea annulus, Nerita albicilla, Morula margariticola* and the opisthobranch *Jorunna tomentosa.*

Micromolluscs found in drift in sandy patches among the coral slabs were a mixture of lagoon and seaward species; none were found alive and their occurrence is attributed to transport from both the seaward reefs and the patch reefs in the lagoon.

Shallow, subtidal patch reefs covered about 35 percent of the lagoon floor. Attached to much of the coral (*Porites* and *Acropora*) were *Turbinaria, Halimeda,* and filamentous green algae. *Cypraea moneta, Conus lividus,* and *Cymatium muricinum* were the most conspicuous epifaunal gastropods (Fig. 15) but the micromollusc *Diala flammea* was also an important constituent of the fauna, forming up to 90 percent of the species composition of coral washings. The numbers of bivalves were not counted, but four were obviously abundant; *Electroma* sp. was the dominant bysally attached form on *Acropora* and *Porites,* with *Ostrea sandvicensis* in lesser numbers; *Cardita variegata* and *Barbatia decussata* were the most abundant attached species on the undersurfaces of coral blocks. The gastropod : bivalve ratio was 81 : 19; of the prosobranch species, 30 percent were algal feeders, 65 percent active predators, and 5 percent faunal grazers. The infauna around the coral included *Nassarius arcularis, Trapezium oblongum,* and *Periglypta reticulata.*

Sediment samples from the lagoon floor (Fig. 1, *L–D*) were characterized by the micromolluscs *Diala flammea* and *Obtortio pyrrhacme* which were also abundant on the sandy reef flat, another species of *Obtortio,* and two species of the pyramidellid *Turbonilla* (Fig. 13). None were found alive. The gastropod : bivalve ratio in this assemblage was 89 :11, and the prosobranch : opisthobranch ratio was 69 : 31.

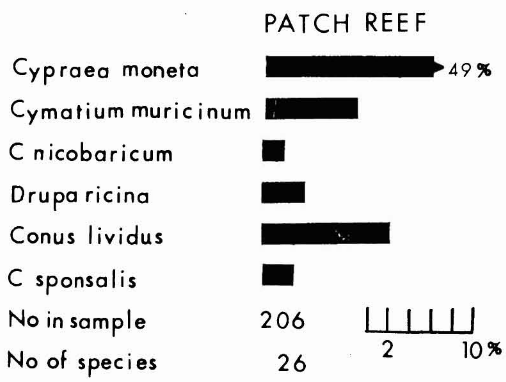

FIG. 15. The assemblage of macromolluscs from patch reefs in the lagoon.

The deep, clear water of the western lagoon (Fig. 1, *L–C*) supported a more diverse macromolluscan fauna than did either the reef flat or the patch reefs. No attempt was made to analyze this assemblage during the study, but the massive coral growth at depths of 8 to 10 m harbored such species as *Pinctada margaritifera, Terebra maculata, Atrina vexillum, Spondylus ducalis,* and *Tridacna maxima.*

COMPARISON OF SEAWARD REEF AND LAGOON MOLLUSCS

Two features of the molluscan species composition of the seaward reefs and lagoon are salient: the seaward reef fauna was more homogeneous than that of the lagoon, and few species occurred both on the seaward reef and in the lagoon. Among the macromolluscs, 17 percent were at home both on the seaward reef and in the lagoon; whereas this is true for only 14 percent of the micromolluscs. The figures may be somewhat generous, however, and if those species which occurred only very rarely in either area (for example 140 shells of *Hiloa* in the lagoon versus eight on the seaward reefs) are omitted, the overlap for both macro- and micromolluscs was about 9 percent.

Most of the overlap was among the molluscs of the patch reefs. Species in apparently equal abundance on the seaward reefs and on the patch reefs were *Morula anaxeres, Conus pulicarius, Conus lividus,* and *Coralliophila neretoides. Drupa ricina* was far more abundant on the seaward reefs than on the patch reefs; *Cypraea moneta* was more numerous on patch reefs. *Cymatium muricinum* and *C. nicobaricum* appeared to be more often associated with the patch reefs than the seaward reefs, but *Bursa* spp. were more often on the seaward reefs.

More species were recorded from the seaward reefs than from the lagoon, but individual numbers were low compared with the abundance of some lagoon species. The seaward reef molluscs were predominantly gastropod and epifaunal. The lagoon molluscs included both epifaunal and infaunal forms, and there was a corresponding increase in the number of bivalves in proportion to gastropods, and of opisthobranchs in proportion to prosobranchs.

FAUNAL COMPOSITION

The Fanning Island molluscan faunal list consists of approximately 265 species of littoral marine forms; although the list cannot be considered complete, the collections were extensive (more than 6,000 specimens were analyzed for this study), and, with the exception of the rather cursory observations of the deep reefs near English Harbor pass and of the windward reefs, the present record is considered fairly representative of the fauna. If the species recorded from the Line Islands during the Whippoorwill Expedition (Bernice P. Bishop Museum collections) are added to my list, the Line Island molluscan fauna is composed of about 305 species (Table 1). This figure may be compared with those reported for other atolls: 504 for the Cocos Keeling Islands, Indian Ocean (Maes, 1967); 420 for Funafuti, Ellice Islands (Hedley, 1899*a*); and an estimated 500 to 600 for the Tuamotus (Morrison, 1954; Salvat, 1967).

Although distance has traditionally been cited as a primary cause of attenuation (Hedley, 1899 *b*; Salvat, 1967; Cernohorsky, 1970), it is difficult to reconcile this explanation with the occurrence of *Cassis* and *Siphonaria* at as far-flung an Indo-West-Pacific outpost as Hawaii, and with the records of *Oliva, Harpa, Planaxis sulcatus,* and *Asaphis violascens* from islands in the Line group other than Fanning. Nor does the distance-effect account for distributional anomalies: the patchy occurrence of *Thais aculeata* and *Engina mendicaria* on seaward reef flats, and the very rare occurrence of *Littorina undulata* and *Strombus* spp. (four specimens, only one of which was collected alive, were recorded during this expedition). That nutrients may be a factor in the occurrence of marine molluscs has been suggested by Maes (1967); however, the high concentrations of total and particulate organic carbon in the water at Fanning and the extraordinary magnitude of photosynthetic production reported for the atoll (Gordon, Pacific Science, this issue) may possibly preclude this factor as a determinant of faunal composition. Lack of topographical diversity was proposed by Morrison (1954) to account for the short faunal lists of atolls, and Kohn (1967) has stated that habitat diversity is a more important factor in determining species diversity in *Conus* than are longitudinal gradients.

Two features of the Fanning Island molluscan faunal lists are consistent with those reported for other insular faunas. The gastropod : bivalve ratio of 81 : 19 was similar to that reported for the Hawaiian Islands (Kay, 1967), the Cocos Keeling Islands (Maes, 1967), and Niue Island (Cernohorsky, 1970), and is on the order of that which has been proposed as a general characteristic of insular faunas (Kay, 1967). The virtual absence of scaphopods, cephalopods, and amphineurans is also consistent with the small numbers of these groups mentioned in the faunal lists of other islands (Kay, 1967; Maes, 1967; Cernohorsky, 1970). Faunal lists, however, are singularly uninformative with respect to the distribution and abundance of species. The following discussion is, therefore, directed toward ascertaining the sources of attenuation at Fanning.

The molluscs of the littorine zone form a well known ecological assemblage throughout the world, and include not only littorines but nerites, archaeogastropod limpets, pulmonate limpets, and *Planaxis sulcata.* As many as three littorines, three nerites, two archaeogastropod limpets, and two pulmonate limpets have been reported in the assemblage in various parts of the Indo-West-Pacific (see Kalk, 1958; Purchon and Enoch, 1954; Taylor, 1968). Among some islands of the Pacific, however, the assemblage appears to be fairly simple. In the Tuamotus *Littorina coccinea, Tectarius grandinatus,* and *Nerita plicata* are found in the zone above the seaward reefs (Morrison, 1954; Salvat, 1967). At Kwajalein and Majuro in the Marshall Islands, *Littorina coccinea, L. undulata,* and *Nerita plicata* occurred along seaward shorelines and *Siphonaria, Peasiella,* and *Planaxis sulcata* occurred in patches along the lagoon and in the passes (Kay, unpublished). At Fanning where a single littorine and nerite were found on seaward shorelines and where only occasional clusters of *Littorina scabra* and very rarely specimens of *L. undulata* were found, in addition, along lagoon shores, the composition of the littorine zone appears to be one of the simplest recorded.

The molluscs of seaward reef flats may be similarly examined. In an analysis of the marine molluscs of the Tuamotus, Salvat (1967) noted that seaward reefs exhibit a topographical and faunal homogeneity but did not list the molluscs. A standard set of species can be proposed for seaward reef flats in the Pacific, the list of 22 species (Table 2) which appear rather consistently in the faunal lists for the Tuamotus (Morrison, 1954; Chevalier et al., 1968); at Onotoa, Gilbert Islands (Banner, 1952); at Kwajalein and Majuro, Marshall Islands (Kay, unpublished); and at Fanning. Of these, 17 species were abundant on the reefs at Fanning, two (*Thais aculeata* and *Cypraea annulus*) occurred but were much restricted in their occurrence, and two (*Cerithium spp.* and *Dendropoma maximum*) did not appear to occur at Fanning. Based on this analysis, the molluscan assemblages of the Fanning seaward reefs appear to show little attenuation.

The fauna of the lagoon is more difficult to discuss, for as Salvat (1967) has pointed out for the Tuamotus, no two atolls have identical lagoon faunas, and he suggests that it is the lagoon fauna which characterizes each atoll. Comparison of the Fanning Lagoon with those of the Tuamotus and that of Funafuti demonstrates the dissimilarities: of the 34 species listed for Raroia (Morrison, 1954), only 15 occurred in the Fanning Lagoon; of the 13 common species mentioned for Mururoa (Chevalier, et al., 1968), only six occurred at Fanning; and of the 51 species cited as common or abundant at Funafuti (Hedley, 1899 *a*), only 23 occurred at Fanning.

The distinction between open and closed lagoons has been drawn for the atolls of the Tuamotus; in open lagoons there is a greater variety of molluscan species but the species occur in lesser numbers than in closed lagoons (Salvat, 1967). Lagoon topography is, however, more complex than is indicated by the terms "open" and "closed." Some lagoon reefs resemble seaward reefs, on others there are beds of *Thalassia, Cymodocea,* or *Halophila,* or mangrove swamps encroach on the reef (Wells, 1957). Lagoon slopes are often covered by talus or thick coral growth (Wells, 1957). If each of these features also harbors one or more molluscan assemblages, then the rather short list of molluscs reported from Fanning may reflect the somewhat simplified topography of the lagoon.

The hypothesis serves both to explain features of the Fanning Island faunal list and to predict features for other atolls. The apparent absence of *Asaphis* and *Planaxis sulcata* and the rare occurrence of *Strombus* and *Lambis* may be associated with the absence of the topographical features which determine the occurrence of these molluscs. The small amount of overlap between seaward reef and lagoon molluscs may be attributed to the lack of appropriate lagoon reef at Fanning. And one may predict that in those lagoons which have extensive seaward-type lagoon reefs, there will be a greater degree of overlap between seaward reef and lagoon faunas than occurs on atolls which do not have such reefs.

It should also be practical to extend the hypothesis to include physical features of the seaward reefs. Refined sampling techniques will undoubtedly delimit molluscan assemblages on the seaward reefs which are not recognized in this rather general survey. With smaller assemblages, the restricted distribution of certain species and the rare occurrence of others may also be explicable in terms of topographical features.

Topographical diversity is not considered a panacea to account for faunal composition among Pacific islands. The history of the occurrence of an organism (that is, time of arrival), the history of the atoll itself, community structure, competition, and other biotic factors are essential parts of the picture. The hypothesis does have the advantages, however, of being testable, and of directing attention to more specific aspects of molluscan distribution than have heretofore been recognized.

FAUNAL RELATIONSHIPS

The faunal relationships of the Line Island molluscs are most conveniently discussed in terms of three groups of species: those which are distributed apparently with equal abandon

TABLE 1

LIST OF MOLLUSCS FROM THE LINE ISLANDS

CLASS, FAMILY, AND SPECIES	FANNING SEA	FANNING LAGOON	KING.[1]	PALM.[1]	WASH.[1]	XMAS[1]	JAR.[1]
AMPHINEURA							
Chitonidae							
Chiton sp.	+					+	
GASTROPODA							
Scissurellidae							
Scissurella coronata Watson, 1886	+						
Scissurella sp.	+						
Fissurellidae							
Diodora granifera (Pease, 1861)	+						
Emarginula bicancellata Montrouzier, 1860	+						
Emarginula peasei Thiele, 1918	+						
Hemitoma sp.	+						
Patellidae							
Patella stellaeformis Reeve, 1842	+						
Trochidae							
Euchelus angulatus Pease, 1867	+						
Monilea nucleus (Philippi, 1849)		+					
Monilea sp.	+	+					
Trochus histrio Reeve, 1848	+		+	+		+	
Stomatiidae							
Stomatella rosacea (Pease, 1867)	+						
Turbinidae							
Astrea helicina (Gmelin, 1791)	+		+	+	+	+	
Turbo argyrostomus Linn., 1758	+		+	+	+	+	
Phasianellidae							
Hiloa variabilis (Pease, 1860)	+	+					
Neritidae							
Nerita albicilla Linn., 1758		+		+			
Nerita plicata Linn., 1758	+	+	+	+	+	+	+
Nerita polita Linn., 1758	+			+		+	
Nerita reticulata Karsten, 1789				+			
Neritina bensoni (Recluz, 1850)		+					
Littorinidae							
Littorina coccinea Gmelin, 1791	+	+		+	+		
Littorina scabra Linn., 1758		+		+			
Littorina undulata Gray, 1839		+					
Vitrinellidae							
Lophocochlias minutissimus (Pilsbry, 1921)	+						
Vitrinellids (3 spp.)	+						
Truncatellidae							
Truncatella sp.	+						
Rissoinidae							
Alvania (2 spp.)	+	+					
Rissoina ambigua Gould, 1851	+					+	
Rissoina exasperata Souverbie, 1866	+						
Rissoina miltozona Tomlin, 1915	+						
Rissoina plicata A. Adams, 1851	+						
Rissoina semiplicata Pease, 1863						+	
Rissoina tenuistriata Pease, 1867	+						
Rissoina turricula Pease, 1860	+						

[1] Records from King. (= Kingman Reef), Palm. (= Palmyra), Wash. (= Washington), Xmas (= Christmas), and Jar. (= Jarvis) from Bernice P. Bishop Museum collections.

TABLE 1 (*continued*)

CLASS, FAMILY, AND SPECIES	FANNING SEA	FANNING LAGOON	KING.[1]	PALM.[1]	WASH.[1]	XMAS[1]	JAR.[1]
Assimineidae							
Assiminea nitida Pease, 1864		+					
Architectonicidae							
Heliacus sp.		+					
Vermetidae							
Dendropoma maximum (Sowerby, 1825)						+	
Serpulorbis sp.	+						
Vermetid spp.	+						
Planaxidae							
Planaxis lineatus (Da Costa, 1776)	+	+				+	
Planaxis sulcata Born, 1780				+		+	
Diastomidae							
Obtortio pyrrhacme (Melvill and Standen, 1896)		+					
Obtortio sp.		+					
Diala flammea (Pease, 1867)		+					
Cerithiidae							
Bittium zebrum Kiener, 1841	+						
Cerithium atromarginatum Dautzenberg and Bouge, 1933	+						
Cerithium breve Quoy and Gaimard, 1833		+		+	+	+	
Cerithium columna Sowerby, 1855	+			+	+	+	
Cerithium echinatum Lamarck, 1822	+				+		
Cerithium nesioticum Pilsbry and Vanatta, 1909	+						
Cerithium sculptum Pease, 1869	+						
Rhinoclavis asper (Linn., 1758)		+		+		+	
Rhinoclavis procera (Kiener, 1841)		+				+	
Rhinoclavis sinensis (Gmelin, 1791)		+		+	+	+	
Seila sp.	+	+					
Cerithiopsidae							
Cerithiopsis (2 spp.)	+						
Triphoridae							
Triphora dolicha Watson, 1886	+						
Triphora regalis Jouss., 1884	+						
Triphora violacea Quoy and Gaimard, 1833	+						
Triphora (5 spp.)	+	+					
Viriola cancellata (Hinds, 1843)	+						
Epitoniidae							
Epitonium (2 spp.)	+						
Eulimidae							
Balcis (3 spp.)		+					
Leiostraca sp.	+						
Stiliferidae							
Stilifer sp.	+[2]						
Hipponicidae							
Hipponix conicus (Schumacher, 1817)	+						
Calyptraeidae							
Cheilea equestris (Linn., 1758)						+	
Fossaridae							
Fossarus cumingii (A. Adams, 1853)	+						
Fossarus sp.	+						
Strombidae							
Strombus gibberulus gibbosus (Roding, 1798)		+		+			
Strombus luhuanus Linn., 1758		+		+			

[2] Indicates specimens in Bernice P. Bishop Museum collections.

TABLE 1 (*continued*)

CLASS, FAMILY, AND SPECIES	FANNING SEA	FANNING LAGOON	KING.[1]	PALM.[1]	WASH.[1]	XMAS[1]	JAR.[1]
Strombus maculatus Sowerby, 1842		+		+	+		
Strombus mutabilis mutabilis Swainson, 1821		+					
Lambis chiragra chiragra Linn., 1758	+					+	
Lambis truncata sebae (Kiener, 1843)	+					+	
Ovulidae							
Calpurnus verrucosus (Linn., 1758)						+	
Ovula ovum (Linn., 1758)	+				+	+	
Triviidae							
Pedicularia pacifica Pease, 1865	+						
Proterato sulcifera sohmeltziana (Crosse, 1867)	+						
Trivirostra pellucidula (Gaskoin, 1846)	+						
Trivia sp.	+						
Cypraeidae[3]							
Cypraea annulus Linn., 1758		+		+			
Cypraea arabica Linn., 1758		+	+	+	+	+	
Cypraea asellus Linn., 1758		+					
Cypraea bistrinotata Schild. and Schild., 1937						+	
Cypraea caputserpentis Linn., 1758	+		+	+	+	+	+
Cypraea carneola Linn., 1758	+			+	+	+	
Cypraea childreni Gray, 1825	+					+	
Cypraea chinensis Gmelin, 1791					+	+	
Cypraea cicercula Linn., 1758				+		+	
Cypraea clandestina Linn., 1767		+		+			
Cypraea cribraria Linn., 1758				+			
Cypraea depressa Gray, 1824	+		+	+	+	+	
Cypraea erosa Linn., 1758	+			+		+	
Cypraea fimbriata Gmelin, 1791				+		+	
Cypraea goodalli Sowerby, 1832						+	
Cypraea helvola Linn., 1758	+[2]			+	+	+	
Cypraea irrorata Gray, 1828						+	
Cypraea isabella Linn., 1758	+		+	+	+	+	
Cypraea lynx Linn., 1758		+		+	+	+	
Cypraea maculifera Schilder, 1932				+			
Cypraea mauritiana Linn., 1758	+[2]			+			
Cypraea moneta Linn., 1758	+	+	+	+	+	+	+
Cypraea nucleus Linn., 1758	+				+	+	
Cypraea poraria Linn., 1758	+		+	+	+	+	
Cypraea scurra Gmelin, 1791	+			+	+	+	
Cypraea schilderorum Iredale, 1939	+			+	+	+	
Cypraea stolida Linn., 1758						+	
Cypraea talpa Linn., 1758	+			+	+	+	
Cypraea teres Gmelin, 1791					+	+	
Cypraea testudinaria Linn., 1758					+		
Cypraea tigris Linn., 1758	+	+					
Cypraea ventriculus Lamarck, 1811					+		
Cypraea vitellus Linn., 1758		+[2]				+	
Cassidae							
Casmaria erinaceus kalosmodix (Melv. 1883)				+		+	
Casmaria ponderosa ponderosa (Gmelin, 1791)	+[2]					+	
Cypraecassis rufa (Linn., 1758)					+		
Tonnidae							
Tonna perdix (Linn., 1758)				+	+	+	+
Malea pomum (Linn., 1758)				+	+	+	+

[3] Other species of *Cypraea* reported from various islands in the Line group include *C. argus* Linn., 1758; *Cypraea dillwyni* Schilder, 1922; *C. globulus* Linn., 1758; *C. mappa* Linn., 1758; *C. mariae* Schilder and Schilder, 1927; and *C. serrulifera* Schilder and Schilder, 1938 (Jewell, 1962).

TABLE 1 (*continued*)

CLASS, FAMILY, AND SPECIES	FANNING SEA	FANNING LAGOON	KING.[1]	PALM.[1]	WASH.[1]	XMAS[1]	JAR.[1]
Naticidae							
Natica marochiensis Gmelin, 1791		+		+			
Natica robillardi Sowerby, 1893		+					
Polinices mammilla (Linn., 1758)		+		+			
Polinices melanostoma (Gmelin, 1791)		+		+		+	
Cymatiidae							
Charonia tritonis (Linn., 1758)	+			+		+	+
Cymatium gemmatum (Reeve, 1844)		+	+	+	+		
Cymatium muricinum (Röding, 1798)		+		+			
Cymatium nicobaricum (Röding, 1798)		+		+	+	+	
Cymatium pileare (Linn., 1758)		+		+		+	
Bursidae							
Bursa bubo (Linn., 1758)					+		
Bursa bufonia (Gmelin, 1791)	+			+	+	+	+
Bursa cruentata (Sowerby, 1835)						+	
Bursa granularis (Röding, 1798)	+			+	+	+	+
Muricidae							
Chicoreus torrefactus (Sowerby, 1841)						+	
Chicoreus sp.	+						
Thaisidae							
Drupa morum Röding, 1798	+		+	+	+	+	+
Drupa ricina (Linn., 1758)	+		+	+	+	+	+
Drupella cornus (Röding, 1798)				+		+	
Drupina grossularia (Röding, 1798)	+		+	+	+	+	+
Drupina rubusidaeus (Röding, 1798)	+						
Maculotriton digitalis (Reeve, 1844)	+	+	+	+	+	+	+
Morula anaxeres (Kiener, 1835)	+	+					
Morula cariosa (Wood, 1828)		+		+		+	
Morula sp. cf. *chaidea* (Duclos, 1832)				+			
Morula crossei Lienard, 1874				+			
Morula granulata (Duclos, 1832)	+	+	+	+	+	+	+
Morula margariticola (Broderip, 1832)		+		+		+	
Morula ochrostoma (Blainville, 1832)				+		+	
Morula uva (Röding, 1798)	+		+	+	+	+	+
Nassa serta (Bruguiere, 1799)		+		+	+	+	
Thais aculeata (Deshayes in Milne-Edwards, 1844)	+			+	+		
Thais armigera (Link, 1807)	+			+	+	+	
Thais intermedia (Kiener, 1836)	+						
Vexilla vexillum (Gmelin, 1791)					+	+	
Coralliophilidae							
Coralliophila violacea (Kiener, 1836)	+	+					
Coralliophila (2 spp.)	+	+					
Magilus fimbriatus (A. Adams, 1852)	+						
Magilus sp.					+	+	+
Quoyula madreporarum (Sowerby, 1834)	+	+		+		+	
Vasidae							
Vasum armatum (Broderip, 1833)	+				+		
Colubrariidae							
Colubraria sp.						+	
Buccinidae							
Caducifer truncatus (Hinds, 1844)	+						
Cantharus farinosus (Gould, 1849)						+	
Cantharus undosus (Linn., 1758)		+			+	+	+
Engina maculata Pease, 1869	+						
Engina mendicaria (Linn., 1758)	+			+	+	+	

TABLE 1 (*continued*)

CLASS, FAMILY, AND SPECIES	FANNING SEA	FANNING LAGOON	KING.[1]	PALM.[1]	WASH.[1]	XMAS[1]	JAR.[1]
Engina tuberculosa Pease, 1863	+						
Pisania billeheusti (Petit, 1853)						+	
Pisania tritonoides (Reeve, 1846)	+		+	+			
Nassariidae							
Nassarius gaudiosus (Hinds, 1844)	+						
Nassarius ravidus (A. Adams, 1851)						+	
Nassarius graniferus (Kiener, 1834)	+						
Columbellidae							
Euplica turturina (Lam., 1822)	+	+				+	
Euplica varians (Sowerby, 1832)	+	+		+		+	
Mitrella rorida (Reeve, 1859)	+	+					
Seminella varia (Pease, 1861)	+						
Fasciolariidae							
Latirus amplustris Dillwyn, 1817	+			+	+	+	+
Latirus iris Lightfoot, 1786	+			+	+	+	+
Peristernia gemmata Reeve, 1847	+					+	
Peristernia nassatula (Lamarck, 1822)	+						
Fasciolaria filamentosus (Röding, 1798)							+
Harpidae							
Harpa amouretta Röding, 1798						+	
Olividae							
Oliva sp.						+	
Marginellidae							
Cysticus sp.	+						
Marginellids (3 spp.)	+	+					
Kogomea sandwichensis (Pease, 1861)	+	+					
Mitridae							
Imbricaria conovula (Q. and G., 1833)	+						
Imbricaria punctata (Swainson, 1821)	+						
Mitra auriculoides Reeve, 1845	+	+					
Mitra cucumerina Lamarck, 1811	+		+	+			
Mitra litterata (Lamarck, 1811)	+	+		+	+	+	+
Mitra mitra (Linn., 1758)	+						
Mitra ferruginea Lamarck, 1811	+						
Mitra stictica (Link, 1807)	+			+	+	+	+
Pterygia nucea (Gmelin, 1791)				+			
Pusia consanguinea (Reeve, 1845)						+	
Strigatella acuminata (Swainson, 1824)		+	+			+	+
Strigatella paupercula (Linn., 1758)		+		+			
Strigatella oleacea (Reeve, 1844)			+			+	
Conidae							
Conus catus Hwass in Brug., 1792	+			+	+	+	+
Conus chaldaeus (Röding, 1798)	+			+	+	+	
Conus ebraeus Linn., 1758	+			+	+	+	+
Conus eburneus Hwass in Brug., 1792						+	
Conus flavidus Lamarck, 1810	+						
Conus lividus Hwass in Brug., 1792	+	+		+	+	+	
Conus miles Linn., 1758						+	
Conus miliaris Hwass in Brug., 1792	+			+			
Conus nussatella Linn., 1758						+	
Conus pulicarius Hwass in Brug., 1792	+	+		+		+	
Conus rattus Hwass in Brug., 1792	+			+	+		+
Conus retifer Menke, 1829	+					+	+
Conus sponsalis Hwass in Brug., 1792	+		+	+	+	+	+

TABLE 1 (*continued*)

CLASS, FAMILY, AND SPECIES	FANNING		KING.[1]	PALM.[1]	WASH.[1]	XMAS[1]	JAR.[1]
	SEA	LAGOON					
Conus tulipa Linn., 1758	+		+	+	+	+	+
Conus virgo Linn., 1758		+					
Terebridae							
Terebra affinis Gray, 1834	+			+		+	
Terebra argus Hinds, 1844		+		+			
Terebra cerithina Lamarck, 1822				+		+	
Terebra chlorata Lamarck, 1822						+	
Terebra crenulata (Linn., 1758)		+		+		+	
Terebra dimidiata (Linn., 1758)				+		+	
Terebra maculata (Linn., 1758)		+		+		+	
Terebra subulata (Linn., 1767)		+		+		+	
Turridae							
Anarithma metula (Hinds, 1843)	+						
Anacithara angiostoma Pease, 1868	+						
Carinapex minutissima (Garrett, 1873)	+						
Daphnella interrupta Pease, 1860	+						
Etrema sp. cf. *scalarina* (Desh., 1863)	+						
Kermia pumila (Mighels, 1845)	+						
Macteola sp. cf. *thiasotes* (Melv. and Standen, 1897)	+						
Tritonoturris sp.	+						
Turrids (7 spp.)	+						
Pyramidellidae							
Odostomia (2 spp.)		+					
Pyramidella sp.	+	+					
Turbonilla (2 spp.)		+					
Aplysidae							
Dolabrifera dolabrifera (Rang, 1828)	+	+					
Atyidae							
Atys cylindrica (Helbling, 1779)		+				+	
Cylichna pusilla (Pease, 1860)		+					
Scaphandridae							
Acteocina sandwichensis (Pease, 1860)	+	+					
Acteonidae							
Pupa sp. cf. *solidula* (Linn., 1758)		+					
Retusidae							
Retusa sp.		+					
Hydatinidae							
Haminea sp.		+					
Dorididae							
Dendrodoris nigra (Stimpson, 1856)		+					
Jorunna tomentosa (Cuvier, 1804)		+					
Aeolididae							
Aeolids (2 spp.)	+	+					
Oxynoidae							
Lobiger sp.	+						
Ellobiidae							
Melampus sp.	+	+					
Melampus luteus Quoy and Gaimard, 1833	+	+					
BIVALVIA							
Limopsidae							
Cosa sp.		+					
Arcidae							
Acar plicata (Dillwyn, 1817)	+	+					

TABLE 1 (*continued*)

CLASS, FAMILY, AND SPECIES	FANNING SEA	FANNING LAGOON	KING.[1]	PALM.[1]	WASH.[1]	XMAS[1]	JAR.[1]
Barbatia decussata (Sowerby, 1833)		+					
Barbatia parva (Sowerby, 1833)	+	+					
Mytilidae							
Modiolus metcalfei Reeve, 1858	+				+	+	
Lithophaga nasuta (Philippi, 1846)	+						
Lithophaga sp.	+						
Isognomonidae							
Isognomon isognomon (Linn., 1758)		+					
Isognomon perna (Linn., 1767)	+	+		+	+	+	
Pteriidae							
Electroma sp.		+					
Pinctada margaritifera (Linn., 1758)		+			+	+	+
Pinnidae							
Atrina vexillum (Born, 1778)		+		+		+	
Pinna muricata Linn., 1758		+				+	
Pectinidae							
Chlamys cuneatus (Reeve, 1853)						+	
Chlamys sp.	+						
Gloripallium pallium (Linn., 1758)						+	
Spondylidae							
Spondylus ducalis Röding, 1798		+				+	
Spondylus (2 spp.)	+						
Limidae							
Lima fragilis (Gmelin, 1791)		+					
Ostreidae							
Ostrea hanleyana Sowerby, 1871	+						
Ostrea sandvicensis Sowerby, 1871		+		+	+	+	
Chamidae							
Chama imbricata Broderip, 1834		+		+			+
Lucinidae							
Codakia divergens (Philippi, 1850)		+				+	
Codakia punctata (Linn., 1758)		+					
Wallucina sp. cf. *gordoni* (E. A. Smith, 1886)		+					
"*Lucina*" *edentula* (Linn., 1758)		+					
Erycinidae							
Kellia sp.	+						
Erycinid sp.		+					
Carditidae							
Cardita variegata (Brug., 1792)		+					
Cardiidae							
Cardium sp.		+					
Fragum fragum (Linn., 1758)		+		+		+	
Mesodesmatidae							
Rochefortina sandwichensis Smith, 1885	+						
Tridacnidae							
Tridacna maxima (Röding, 1798)	+	+		+	+	+	+
Trapeziidae							
Trapezium oblongum (Linn., 1758)		+		+	+	+	
Sanguinolariidae							
Asaphis violascens (Forskal, 1775)				+		+	
Tellinidae							
Arcopagia scobinata (Linn., 1758)		+				+	
Quidnipagus palatam Iredale, 1929		+					

TABLE 1 (*continued*)

CLASS, FAMILY, AND SPECIES	FANNING		KING.[1]	PALM.[1]	WASH.[1]	XMAS[1]	JAR.[1]
	SEA	LAGOON					
Pharaonella tongana (Quoy and Gaimard, 1833)		+					
Pinguitellina pinguis (Hanley, 1845)		+					
Scissulina dispar (Conrad, 1837)		+		+		+	
Semelangulus sp.		+					
Tellinids (4 spp.)		+					
Veneridae							
Lioconcha hebraea (Lamarck, 1818)				+		+	
Periglypta reticulata (Linn., 1758)		+			+	+	
Pitar prora (Conrad, 1837)		+		+		+	
Diplodontidae							
Diplodonta sp.		+					

throughout the Indo-West-Pacific; those which are endemic to the Pacific basin; and those which are endemic to Polynesia. Polynesia is here recognized as including the Cooke, Society, and Tuamotu islands and extending to Easter Island (Schilder and Schilder, 1939). Indo-West-Pacific species form 86 percent, Pacific endemics 12 percent, and Polynesian endemics 2 percent of the fauna. The figures cited are based only on those species for which the distribution is known.

One Polynesian endemic and two which are questionably referred to Polynesia in concert distinguish the Line Island fauna from that of the Phoenix, Gilbert, Marshall, and Hawaiian islands: the common occurrence of *Vasum armatum, Latirus amplustris,* and *L. iris* on the seaward reefs. *Vasum armatum* is endemic to

TABLE 2

SEAWARD REEF GASTROPODS IN THE PACIFIC

Patella stellaeformis Reeve, 1842
Turbo argyrostomus Linn., 1758 (and/or *T. setosus* Gmelin, 1791)
Cerithium spp. (for example, *C. alveolus* Hombron and Jacquinot, 1841 or *C. sejunctum* Iredale, 1929)
Dendropoma maximum (Sowerby, 1825)
Cypraea caputserpentis Linn., 1758
Cypraea depressa Gray, 1824
Cypraea annulus Linn., 1758
Cypraea moneta Linn., 1758
Maculotriton digitalis (Reeve, 1844)
Drupa morum Röding, 1798
Drupa ricina (Linn., 1758)
Drupina grossularia (Röding, 1798)
Morula granulata (Duclos, 1832)
Morula uva (Röding, 1798)
Vasum spp. (*V. armatum* is Polynesian; two other species elsewhere)
Engina mendicaria (Linn., 1758)
Euplica varians (Sowerby, 1832)
Conus ebraeus Linn., 1758
Conus sponsalis Hwass in Brug., 1792
Mitra litterata Lamarck, 1811
Thais aculeata (Deshayes in Milne-Edwards, 1844)

the Tuamotu, Phoenix, and Line islands (Abbott, 1959). The distribution of the two species of *Latirus* is not known. *L. amplustris* was described from Anaa (Tuamotus) and *L. iris* from Tahiti; neither appear in collections I have seen from the Tuamotus, and, indeed, Morrison (1954) records *L. nodatus,* the Pacific basin fasciolarid, in the lagoon at Raroia. *L. amplustris* and *L. iris* are common at Baker and Howland, outliers of the Gilbert Islands, but not at Canton in the Phoenix Islands (Kay, unpublished). The Baker and Howland fauna differs from that of the Line Islands, however, in that *Vasum turbinellus* (Linn., 1758) is the common vasid, and, in addition, *Cantharus undosus,* which is rare in the Line Islands, is a prominent component of the reef fauna.

In most respects the Line Islands fauna appears more closely related to that of the Central Pacific (Gilbert, Phoenix, and Marshall islands) than to that of either Polynesia or Hawaii. It lacks, for example, several Polynesian cowries (*Cypraea obvelata*), and none of the Hawaiian endemic molluscs are recorded from the Line Islands.

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LITERATURE CITED

ABBOTT, R. T. 1959. The family Vasidae in the Indo-Pacific. Indo-Pacific Mollusca, vol. 1, pp. 15–32, pls. 1–10.

BAKUS, G. J. 1964. The effects of fish-grazing on invertebrate evolution in shallow tropical waters. Occasional Papers of the Allan Hancock Foundation, no. 27, pp. 1–29.

BANNER, A. H. 1952. Preliminary report on the marine biology of Onotoa atoll, Gilbert Islands. Atoll Research Bulletin, vol. 13, pp. 1–42.

CHEVALIER, J. P., M. DENIZOT, J. L. MOUGIN, Y. PLESSIS, and B. SALVAT. 1968. Étude géomorphologique et bionomique de l'atoll de Mururoa (Tuamotu). Cahiers du Pacifique, no. 12, pp. 1–144, 24 pls.

CERNOHORSKY, W. O. 1970. The littoral marine molluscs of Niue Island. Records of the Auckland Institute and Museum, vol. 7, pp. 175–186.

DEMOND, J. 1957. Micronesian reef-associated gastropods. Pacific Science, vol. 11, pp. 275–341, 4 pls.

EKMAN, S. 1953. Zoogeography of the sea. Sidgewick and Jackson, London. i–xiv + 1–417.

GORDON, D. C. 1971. Organic carbon budget of Fanning Island Lagoon. Pacific Science, vol. 25, no. 2, pp. 222–227, 4 figs.

GORDON, D. C., and H. SCHIESSER. 1970. Temperature, salinity, and oxygen observations at Fanning Island. Hawaii Institute of Geophysics Report 70-23.

GUINTHER, E. B. 1971. Ecologic observations on an estuarine environment at Fanning Atoll. Pacific Science, vol. 25, no. 2, pp. 249–259, 4 figs.

HEDLEY, C. H. 1899 *a.* Mollusca of Funafuti. 3 pts. Memoirs of the Australian Museum, vol. 3, pp. 397–565.

——— 1899 *b.* Zoogeographic scheme for the mid-Pacific. Proceedings of the Linnaean Society of New South Wales, vol. 24, pp. 391–417.

JEWELL, H. 1962. Marine mollusks from the Line Islands. Hawaiian Shell News, vol. 11, no. 2, p. 4.

KALK, M. 1958. Ecological studies on the shores of Moçambique. I. The fauna of the intertidal rocks at Inhaca Island, Delagoa Bay. Annals of the Natal Museum, vol. 14, pp. 189–229, 2 pls.

KAY, E. A. 1967. The composition and relationships of the marine molluscan fauna of the Hawaiian Islands. Venus, vol. 25, pp. 94–104.

KOHN, A. J. 1967. Environmental complexity and species diversity in the gastropod genus *Conus* on Indo-West-Pacific reef platforms. American Naturalist, vol. 101, pp. 251–259.

MAES, V. O. 1967. The littoral marine mollusks of Cocos Keeling Islands (Indian Ocean). Proceedings of The Academy of Natural Sciences of Philadelphia, vol. 119, pp. 93–217, 26 pls.

MORRISON, J. P. E. 1954. Animal ecology of Raroia atoll, Tuamotus. I. Ecological notes on the mollusks and other animals of Raroia. Atoll Research Bulletin, vol. 34, pp. 1–28.

MORTON, J. E., and D. A. CHALLIS. 1969. The biomorphology of Solomon Islands shores with a discussion of zoning patterns and ecological terminology. Philosophical Transactions of the Royal Society of London, series B, vol. 225, pp. 459–516.

PURCHON, R. D., and I. ENOCH. 1954. Zonation of the marine fauna and flora on a rocky shore near Singapore. Bulletin of the Raffles Museum, vol. 25, pp. 47–65.

SALVAT, B. 1967. Importance de la faune malacologique dans les atolls polynesiens. Cahiers du Pacifique, no. 11, pp. 7–49, 7 figs., 12 photos.

SCHILDER, F. A., and M. SCHILDER. 1939. Prodrome of a monograph on living Cypraeidae. Proceedings of the Malacological Society of London, vol. 24, pp. 182–231.

STEPHENSON, T. A., and A. STEPHENSON. 1949. The universal features of zonation between tidemarks on rocky coasts. Journal of Ecology, vol. 37, pp. 289–305.

TAYLOR, J. D. 1968. Coral reef and associated invertebrate communities (mainly molluscan) around Mahé, Seychelles. Philosophical Transactions of the Royal Society of London, series B, vol. 254, pp. 129–206, 20 figs., pls. 13–17.

WELLS, J. W. 1957. Coral reefs. In: J. W. Hedgepeth, ed., Treatise on marine ecology and paleocology, vol. 1. Memoirs, Geological Society of America, vol. 1, pp. 609–631, 2 figs., 9 pls.