18. Notes on Pacific Land Snails.

By Dr. C. Montague COOKE, Jr., Ph. D., Curator,
Bishop Museum, Honolulu.

The land fauna and flora of the Pacific offer a problem in distribution that is growing not only in interest but in importance. Whether they give evidence of dispersal by drift or other natural means or of the presence of larger land areas at an earlier geological period are questions that no one can attempt to answer until we have much larger or more exact collections than have yet been assembled. It is also necessary to have much greater knowledge of the under-water topography of the floor of the Pacific and, in addition, of the geology of each of the groups of islands, together with data on the amount of rising and sinking of these groups.

Very few orders of land animals are represented on the central and southeastern islands of the Pacific, and undoubtedly more has been written on land snails than on any other order. Pilsbry and Hedley have suggested former land connection as the reason for their present distribution. Except in the case of a few families, our knowledge at present is based on very insufficient data. Only the larger and more showy shells have been adequately collected in the few islands that have been visited by conchologists, and the distribution of some of the genera of these larger snails is quite accurately known.

As an example of how little collecting has already been done, let me cite the Fiji Islands. This group is made up of 155 islands, excluding the smaller islets. Of these only 30 have shells reported from them. Of the 30 one only has more than 40 species, 2 have between 20 and 25 species, 3 have 10 to 15 species, 4 have 6 to 9 species, and 20 have less than 5 species.

As another example, there are 11 islands in the Marquesas. Six of these have not had a single shell reported from them. Hiva Oa has 19 species, Nuka Hiva 9, Huapu and Tahuata 3, and Fatuhiva 1. Undoubtedly each of the islands has a much richer fauna than what is known from Hiva Oa at present.

In the Tongan Islands, shells have been reported from only three islands, two of these, Tongatabu and Haafeva, being comparatively low coral islands, Vavau a limestone island 670 feet in elevation. From the more important high and volcanic islands of the western and northern parts of the group, not a single snail has been reported.

Since 1890 very few species of land snails have been added to the lists known to inhabit the islands of the central and southeastern Pacific. In the Fiji Islands only one paper has been published, by Gude, since 1887, when Garrett's paper dealing with Fijian shells appeared. A good deal has been added to our intimate knowledge of *Partula* by the researches of Crampton, and a number of new species have been described by Pilsbry in various volumes of the Manual of Conchology. Most of the material from which this paper has been gathered is from publications by Garrett and Pilsbry, which are among the few sources of information on the subject contained in the library of the Bishop Museum. This information has been increased somewhat by small collections made for the Bishop Museum since 1920. Though these sources are incomplete I think that any additional literature that I have missed would not materially change the conclusions.

It has been extremely difficult to reconcile the genera as understood by one author with those of another. In the family Zonitidae, for example, various authors have ascribed Asiatic genera to the islands of the Pacific as far north as Hawaii and as far east as the Marquesas. Before it is possible to determine whether these genera really occur throughout these islands it will be necessary to make anatomical studies of the animals. In my opinion, a number of these genera will need to be dropped from the list of the region under discussion and new genera established. Unfortunately, very few animals of these snails have been preserved, and it is to be hoped that future collectors will bear this point in mind so that a fairly adequate understanding of the genera of the Pacific can be gained through a study of their anatomy.

My interpretation of the genus *Microcystis* as dealt with in this paper is a very broad one. For the sake of convenience I have included under this name species referred by different authors to the genera *Philonesia*, *Microcystina*, *Lamprocystis*, *Sitala*, and *Liadetia*. Except for *Philonesia*, the generic limits of none of the Pacific species have been ascertained definitely on anatomical data. In all probability, three to five distinct genera are included in these, either one or two of which are strictly Pacific genera.

I have dealt with the family Tornatellinidae as established by Pilsbry in Volume 23 of the Manual of Conchology. Since this was published, Odhner has shown that the Juan Fernandez species belonged to a different family from other Pacific Tornatellids. Whether the type of the genus *Tornatellina bilamellata* occurs in Juan Fernandez seems to me questionable. The original description gave Rapa as the habitat.

Later authors, Smith, Pfeiffer, and Odhner, have referred a Juan Fernandez shell to this species, but the figure and description given by Kuster seem to me to be closer to the Rapa type of shells than to any of those of Juan Fernandez.

In the genus *Thaumatodon* I have included a genus referred to *Pitys* by Garrett and other authors. The genus *Charopa* as understood by writers on Pacific problems will have to be very materially revised. Undoubtedly species belonging to the genus *Rhytida* have been included by many writers in this genus. Species from the Hawaiian Islands that have been referred to *Pseudohyalina*, *Punctum*, and *Sphyradium* will have to be verified by anatomical dissections.

No accurate work can be done on the distribution problem of the Pacific until all the different genera are accurately defined and their relative position in the families to which they belong given.

The number of species of snails found on each island depends not only on its geological formation but also on its relative age. So far as I know, no recent coral island has an endemic species peculiar to itself. A few species have originally been described from such an island, but later collections have shown them to be widely distributed, as the land shells inhabiting these low islands are found to include four to a dozen species that have been widely disseminated throughout the Pacific by the early Polynesian or later voyagers. The second type is a high coral limestone island. Most of the land shell population of this type of island is made up of the same widely distributed Polynesian snails, with the addition in a few instances of peculiar species and in a few more instances of peculiar varieties or geographical races. The third type of island is composed entirely of continental or igneous rock or of either of these rocks, and more or less covered with coral limestone. It is only on this type of island that almost all the peculiar endemic families, genera, and species are found.

The land snails of the Pacific have apparently been distributed in four distinct waves. The first wave, which consists of the families Partulidae, Achatinellidae, and Amastridae, occurred so long ago that peculiar families have evolved and left no relatives on the continents bordering the Pacific. The second wave is made up of members of the families Zonitidae, Endodontidae, Succineidae, Pupillidae, and Tornatellinidae. These families are represented in the Pacific for the most part by peculiar genera or subgenera, they comprise most of the smaller sized species found throughout the Pacific, and their distribution can be accounted for partly by hurricanes. The third wave is represented by

some of the genera of the second migration that have been carried between different groups of islands and have not yet been differentiated except by species. In the fourth wave, shells were brought at first by the Polynesians and later by commerce and as a result of trading of the Polynesians and white men. There is no doubt that about a dozen species were carried by Polynesians in their migrations. At least four species were carried by the latter to the Hawaiian Islands. These for the most part are minute species of snails that are always found in situations just above high-water mark and are fairly uniformly distributed wherever Polynesians live. Such shells have but one habitat, living on the low flats in a belt between high-water mark up to a few hundred feet elevation. They are abundant in the native villages and in the plantations, being found usually on or under dead coconut leaves and coconut husks. A very small number are found on the leaves of plants, especially the banana in cultivated plantations. These are the only species that are known to occur on the low coral islands and atolls.

As an example of a snail distributed by modern commerce, let me mention *Subulina cotona*. Up to 1887, Garrett knew this species only as an inhabitant of the West Indies. It was not known in Hawaii prior to 1903. Since 1920, specimens have come into the Bishop Museum collection from Rapa, the Marquesas, Society Islands, Cook Islands, Samoa, Fiji, Tonga, and New Hebrides. In Tutuila, this is one of the most abundant species living today occurring in great abundance from the sea-shore to the crest of the mountains.

In most cases the size of a Pacific island seems to have no relation to the number of species of snails inhabiting it. Unfortunately except in the Hawaiian and Society Groups very little systematic collecting has been done up to the present time. The factors of isolation and possibly age seem to have played the more important roles. In the Society Group, there is no doubt that far more collecting has been done on Tahiti than on Raiatea. Yet, according to Garrett's list, Tahiti has 21 peculiar species and Raiatea has 22, although Tahiti has 350 square miles and Raiatea 60. I have been told that some geologists consider that the northwestern group of the Society Islands, consisting of Huahine, Raiatea, Tahaa, Borabora, and Maupiti, is older than the southeastern, which is made up for the most part of Tahiti and Moorea. Fifty-three species are known to be peculiar to Tahiti, which contains 350 square miles, and 39 to Moorea, which contains 390 square miles. That isolation has played an important role is shown by the fact that of the 53 species found in the northwestern group 44 (85 per cent) are peculiar to

one island, while of the 39 species occupying the southeastern group 33 (84 per cent) are peculiar to a single island.

In the Hawaiian Islands the differences due to size are much greater. Hawaii, which covers more than 4,000 square miles, has fewer peculiar species than Molokai with only 261 square miles. Oahu with about 600 square miles has, probably, more than five times the number of species as Hawaii with nearly seven times the area.

The endemicity of the snails of the Pacific islands seems to have a direct relation not only to their size but also to their habits. The great majority of the species more than ten millimeters in size are known to inhabit only a single island. The distribution of most of the species of this size that inhabit more than one island or group of islands is undoubtedly due to human agency and most of these since the white man has entered the region. The distribution of smaller species (most of which are less than five millimeters in length or diameter) is partly due to the Polynesians and partly to natural causes, of which the most important is probably hurricanes. Practically all species of snails that inhabit forests or the higher portions of an island are peculiar to a single island, and with very few exceptions they never get beyond a single group of islands.

I do not think that isolation is the most important factor that has entered into the evolution of Pacific faunas, although it would seem so from the above paragraph. The Fiji Islands are admittedly part of the remnants of a very ancient land mass, as a considerable proportion of their area is made up of continental rocks. From 30 of these islands 89 endemic species have been reported. The Society Group with 7 islands has 101, and the Hawaiian Group of eight islands has about 660. In the region made up of the groups Fiji, Tonga, Samoa, Society, Cook, Tubuai, and the Marquesas, there are known at present 8 peculiar genera. Two of these, *Diglyptus* (in Endodontidae) and *Lamellovum* (in Tornatellinidae), are monotypic genera from the Island of Rapa; one, *Libera* (Endodontidae), from the Society and Cook Groups, and five (Zonitidae), *Parmella*, *Orpiella*, *Fijia*, *Fretum*, and *Irenella*, from the Fijis. From the Hawaiian Group, at least 18 peculiar genera have been recorded, 11 of which belong to the peculiar families Achatinellidae and Amastridae. Excluding the genera belonging to these two families, we have 7 peculiar genera: *Godwinia*, *Nesovitrea* (Zonitidae); *Auriculella*, *Gulickia*, *Tornatellaria* (Tornatellinidae); *Lyropupa* and *Pupoidopsis* (Pupillidae). Of the 18 peculiar genera, 7 have been reported from only one island.

Except for the Island of Rapa and the Fijian Group, no other group of islands has a single peculiar genus.

As an example of a species of shell undoubtedly distributed during former land connections, I should like to cite that of *Partula lyrata*. This species, which belongs to the most distinctive subgenus of *Partula*, is confined to the Lau Group of the Fijis, and the two nearest islands, Lauthala and Taveuni, of the main group. The Lau Group consists of 34 islands and clusters of islets. I think that all geologists agree that at some period these islands formed part of a larger land mass. At the time they were united, the monotypic subgenus *Thakombaua* was evolved. By submergence, some of these islands were not entirely drowned, and since that time they have risen at least 400 feet. This group is made up of six islands almost entirely composed of igneous rock, 17 of mixed igneous and limestone, 13 of limestone, and four of low flat sand islands. Up to the present, *P. lyrata* has been found on only eight of these islands, most of which are in the northern half of the group. It is extremely significant that the eight islands from which this species is known are composed either entirely of igneous rock or else of a mixture of igneous rock and limestone. Whether this species occurs on an island composed entirely of limestone remains to be discovered. I very much doubt that it ever will be. That limestone is not deleterious to the existence of this snail can be easily shown, because on islands made up of igneous and limestone rocks, shells are much more abundant on limestone portions of the island than on igneous portions. This is undoubtedly due to the denser forests in this portion of the islands. Another important fact is that from the few specimens that I have examined from different islands there is not the slightest tendency to form geographical races on each of the separate islands, although these islands must have been isolated for a considerable period of time.

The genus *Partula* is distributed from the Marquesas and Rapa in the southeast to the New Hebrides and Bismark in the southwest and the Caroline Islands, Guam, and the Pelews in the northwest. Pilsbry has divided this genus into nine subgenera. It is very significant that six of these subgenera are limited to single groups of islands. Of the remaining three, one subgenus, that is, *Partula* ss., is found in the Society Islands, Tubuai, and Cook Islands, the last two each with a single endemic species. One subgenus, *Samoana*, includes six species from the Samoan Group and one doubtfully from the Island of Rotuma. The third of the inter-island subgenera, *Melanesica*, has one species on Fiji, 15 on the New Hebrides, 10 on the Solomons, 5 on Bismark and Admiralty, 4 on

Louisade and New Guinea, and 1 on Talauer Island. This subgenus has much the widest distribution of any subgenus in the family; but it partly overlaps the distribution of the genus *Placostylus*. Nearly all the species known of this genus are limited in their distribution to single islands. Unfortunately, the habitats of a number of species are known only from the group of islands on which they occur, so that an accurate chart of the distribution of the species would be impossible with our present knowledge. Wherever a species is known to exist on more than one island these islands are more or less near one another.

The only example of a large species of snail being distributed on more than one group of islands is *Partula hyalina*. This species has been found on Rurutu, Tubuai, and Ravaivai in the Tubuai Group. It is found also on Atiu, Mangaia, Mauke, in the Cook Group, and Tahiti in the Society Islands. I agree with Pilsbry that this species owes its wide distribution to the aid of Polynesian travelers. So far as known at present, all the species of *Partula* are confined to islands of which at least some part is igneous or continental rock, the only exception being *Partula hyalina* from the island of Mauke. That the different species of *Partula* are not easily transported by natural means is shown by the fact that less than 10 of the 99 species of *Partula*, of which we are fairly certain of the group of islands from which they came, are known to occur on more than one islands.

Arguments in favor of larger land areas in the Pacific have been brought forward to explain the distribution of some of the plants and animals. I think it is definitely admitted by most geologists that the dispersal of *Placostylus* in the Solomon Islands, New Hebrides, Fijis, New Caledonia, Lord Howe, and New Zealand can be explained only by former land connections, and I think that some of these land connections have been determined by soundings. That *Placostylus* does occur in the main Fijian Islands and not in the nearby islands of the Lau Group would seem to prove that they cannot drift to islands less than 20 miles distant.

I do not think that the logical distribution of *Partula* on the islands of the Pacific can be explained by the conditions now existing over vast tracts of this ocean. At least since the subgenera and species of this genus have been evolved, no distribution other than the one species *P. lyrata* has occurred and that by man. That this genus at a former period

was able to migrate to islands thousands of miles from the center of origin can be explained only by the supposition that conditions in the Pacific were different at some earlier geological period than they are today. As a result of my study of the distribution of the different genera of land shells I believe these conditions necessarily imply either larger land areas, swifter currents, or an orderly trend of hurricanes, or some factors that are not known to us today.

As an argument against possible continuous land connections at one period is the fact that no two genera occupy exactly the same areas, and in no considerable number of genera do we find an equal amount of evolution of species on any two groups of islands. In small areas a great many cases of an equal amount of evolution has occurred, for example, to mention a few, Tutuila and Upolu, each with three species of *Partula*, the southeastern group of the Society Islands with six species of *Libera* and the northwestern with six species of *Endodonta*; Molokai with one species of the subgenus *Perdicella* and seven of the genus *Newcombia*, and Maui with eight species of *Perdicella* and one of *Newcombia*.

In conclusion I wish to state that our knowledge of the land shell faunas of the Pacific are wholly inadequate. Except for the New Zealand, Hawaiian, Society, Kermedec, and possibly the Cook groups, no serious work has been attempted. At present we do not know the problem of distribution on a single island of the hundreds of islands making up the rest of the groups of the Pacific, not to mention the relations of any one island to the others of its group.

The problem of the land faunas and floras is a rapidly vanishing one. Every day valuable data are being lost. What we need most of all are larger, more accurate collections, and they should be made now. If they are once assembled, students could be found to correlate and interpret the data at some future time, when it will be too late to assemble what we need.

In the not too distant future I trust that the geologists, hydrographers, botanists, and zoologists can get together and paint an historical picture of the Pacific. At present we have only a color chart and very few sample tubes of the colors to be used. I know very well that we could not paint such a picture today.

*	Hawaii		Marquesas		Rapa		Society		Cook		Samoa		Fiji		Fiji (Lau)		Tonga		
	E	P	E	P	E	P	E	P	E	P	E	P	E	P	E	P	E	P	
Parmella													1						
Orpiella													1						
Helicarion			2																
Godwinia	2																		
Fijia													2						
Vitrina	1																		
Nesovitrea	4																		
Vitrea							1						1						*Philonesia*
Pseudohyalina	1																		*Microcystina*
Microcystis	19		6	2	3		6	1	2	2	4		4	6	1		1	2	*Lamprocystis*
Trochonanina			6	2			2	2		2	2	2	3	4			1	2	*Sitala*, *Liardetia*
Kaliella	3																		
Fretum													11						
Irenella													3						
Trochomorpha							4				5		12	1	1		1	1	*Nesophila*
Charopa					1		2	1	10		2	1	4		2		1	1	*Pitys*
Thaumatodon	16		6		1		5		5		2		2		1		1		
Diglyptus					1														
Endodonta	5						6												
Libera							6		3										
Punctum	1																		
Placostylus													13						
Succinea	36		2				8		1		4							1	
Partula			6		1		35	1	1	1	6		2						
Lyropupa	22																		
Nesopupa	19			1			1	1	1		1		1				1		
Pronesopupa	11		1																
Pupoidopsis	1																		
Sphyradium	2																		
Auriculella	29																		
Gulickia	1																		
Elasmias	3			1		1	1	1		1		1						1	
Tornatellina	7	1		3	3			7		6		2	1	2	1			1	
Tornatellides	45			1		1		1		1			1						
Tornatellaria	16																		
Lamellovum					1														
Achatinella	41																		
Partulina	51																		
Newcombia	9																		
Carelia	11																		
Planamastra	1																		
Pterodiscus	4																		
Amastra	143																		
Laminella	15																		
Leptachatina	123																		
Pauahia	3																		
Armsia	1																		
	646	1	29	10	11	2	77	15	23	13	26	6	62	13	6		6	9	
Diplomatina													8						
Mussonia											1		1						
Ostodes											5		3						
Omphalotropis					3		6		3		4		7	4	5		2	1	*Sturanya*
Atropis							5		2										*Aphanoconia*
Scalinella							3												*Orobophana*
Helicina	13		5	1	1	1	10	2	1	1	1	4	8	5	2		2	3	
	13		5	1	4	1	24	2	6	1	11	4	27	9	7		4	4	
	659	1	34	11	15	3	101	17	29	14	37	10	89	22	13		10	13	
% Endemic	99.8%		75.5%		83.3%		85.6%		67.4%		78.7%		80.2%				43.3%		

*E endemic
P widely distributed